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Journal of the Fisheries Research Board of Canada

Some Athecate Hydroids From the Shelf Waters of Northern Canada[1]

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CALDER, D. R. 1972. Some athecate hydroids from the shelf waters of northern Canada. J. Fish. Res. Bd. Canada 29: 217–228.

Sixteen species of athecate hydroids were identified in collections from the shelf waters of northern Canada between the Strait of Belle Isle and the Alaska–Yukon border. This brings the number of athecate species reported from Canada's north coast to 21, and the total number of hydroid species known from the region to 92. One species, *Eudendrium caricum* Jäderholm 1908 is placed in synonymy with *Eudendrium arbusculum* Wright 1859. No high-arctic forms were represented, and only eight of the species are panarctic or low-arctic in distribution. Of the remaining species, six occur in boreal as well as subarctic waters, and two have a wide latitudinal range. Five species, *Corymorpha groenlandica*, *Tubularia regalis*, *Monocoryne gigantea*, *Rhizogeton nudus*, and *Hydractinia monocarpa*, are recorded in North American waters for the first time. These five, plus *Myriothela phrygia*, *Eudendrium capillare*, and the hydroid of *Euphysa*, are new records for northern Canada.

CALDER, D. R. 1972. Some athecate hydroids from the shelf waters of northern Canada. J. Fish. Res. Bd. Canada 29: 217–228.

L'auteur a identifié 16 espèces d'hydroïdes athécates de collections provenant des eaux du plateau continental du Canada septentrional, depuis le détroit de Belle-Isle jusqu'à la frontière Alaska–Yukon. Ceci porte à 21 le nombre d'espèces d'Athecata signalées au large de la côte Nord canadienne, et à 92 le nombre total d'espèces d'hydroïdes connues dans cette région. Une espèce, *Eudendrium caricum* Jäderholm 1908 est classée, à titre de synonyme, avec *Eudendrium arbusculum* Wright 1859. Les formes du Haut-Arctique sont absentes, et seulement huit des espèces énumérées sont panarctiques ou présentes dans le Bas-Arctique. Parmi les autres espèces, six sont présentes dans les eaux boréales aussi bien que subarctiques, et deux ont une vaste répartition latitudinale. Cinq espèces, *Corymorpha groenlandica*, *Tubularia regalis*, *Monocoryne gigantea*, *Rhizogeton nudus* et *Hydractinia monocarpa* sont signalées pour la première fois dans les eaux de l'Amérique du Nord. Ces cinq espèces, en plus de *Myriothela phrygia*, *Eudendrium capillare* et le polype d'*Euphysa* sont des mentions nouvelles pour le Nord canadien.

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OCEANOGRAPHIC and marine biological investigations in Canada's northern shelf waters have been in progress annually since 1947 by personnel of the Fisheries Research Board of Canada. Stations have been occupied aboard M.V. *Calanus* and M.V. *Salvelinus* from the Strait of Belle Isle in eastern Canada to the Alaska border in the northwest. Collections of marine invertebrates have been made from the entire region, the hydroids and bryozoans of which have been deposited in the National Museum of Natural Sciences, National Museums of Canada, Ottawa. The bryozoans of this collection were examined by Powell (1968), and the thecate hydroids by Calder (1970). An account of the athecate hydroids is presented here.

Athecates were found in collections from 26 of the stations occupied in northern Canada between 1947 and 1965 (Table 1, Fig. 1). Sixteen species were identified and are discussed here, including one previously unreported species from northwestern Canada in the collection of the Museum of Natural Sciences. Five of the 16 species are new records for North America: *Corymorpha groenlandica*, *Tubularia regalis*, *Monocoryne gigantea*, *Rhizogeton nudus*, and *Hydractinia monocarpa*. These species, together with *Euphysa* sp., *Myriothela phrygia* and *Eudendrium capillare*, are recorded in northern Canada for the first time.

Combining the present records with those from previous studies, 21 species of athecate hydroids have been reported from the shelf waters of Canada's north coast. This compares with Kramp's (1943) records of 18 species from west Greenland, 13 species from east Greenland, and 19 species from both Iceland and Spitzbergen. Naumov (1960) included about 27 species from the northern seas of the USSR, and Fraser (1937) reported 18 species from the entire Alaska coast. Including the 71 species of thecates reported previously from Canada's north coast (Calder 1970), a total of 92 species of hydroids are known from the region.

Most of the 21 species of athecates recorded from northern Canada have a distinct southern affinity. None are high-arctic in Ekman's (1953) sense (the definitions of "arctic" and "subarctic" followed here are those of Dunbar 1951). Only four species are panarctic, transgressing both arctic and subarctic zones: *Corymorpha groenlandica*, *Tubularia regalis*, *Hydractinia carica*, and *Eudendrium rameum*. Four species correspond with Ekman's (1953) low-arctic category, occurring in the mixed waters of the subarctic: *Monocoryne*

TABLE 1. *Calanus* and *Salvelinus* stations where athecate hydroids were collected.

Station	Location	N	W	Date	Depth (*m*)	Bottom
28	Ungava Bay	58°54.5′	68°59′	19 VII 47	27	Rock
58	"	60 05	65 06	28 VII 48	20	–
103	"	60 24	64 58	6 VII 49	145–255	Rock
201C	"	59 29.5	65 20.5	29 VI 50	80–100	Mud
203	"	58 50	68 18	8 VII 50	30	–
210	Hudson Strait	61 04.5	69 39	21 VII 50	90–110	Rock
225	"	60 40.5	64 39.7	12 VIII 50	22	Rock
226	"	60 38	64 38.9	13 VIII 50	90–100	–
229	Ungava Bay	59 29	65 17.5	26 VIII 50	0–13	–
406	Frobisher Bay	62 74	65 26.5	22 VII 52	46	–
547	Foxe Channel	63 41	80 12	3 IX 53	73	Rock
616	N Hudson Bay	63 15.5	83 41	16 VIII 54	85–90	Rock
811	N Foxe Basin	69 37.2	81 06.3	17 VIII 56	106	Rock
901	N Foxe Basin	69 06	79 11	29 VIII 57	0–34	Mud,sand,rock
59–29	SE Hudson Bay	55 50	80 15	3 VIII 59	37–40	Rock
59–50	"	58 00	79 38	17 VIII 59	50–60	Rock
59–64	"	55 13	82 08	31 VIII 59	23–26	Gravel
61–11	Chesterfield Inlet	63 39	91 27	30 VII 61	20–70	Rock
61–24	Roes Welcome Sound	65 07	86 45	9 VIII 61	44–46	Rock
61–26	Roes Welcome Sound	65 24	86 44	10 VIII 61	40–75	Rock
61–43	Frozen Strait	66 13	85 09	28 VIII 61	85–92	–
62–002	Liverpool Bay	69 49.3	130 19	14 VII 62	0–4	Mud, rock
62–4001	Barrow Strait	74 36	94 13	23 VI 62	35–62	–
65–1048	Dease Strait	69 09.8	106 37	30 VIII 65	60	–
65–1505	Strait of Belle Isle	51 20	56 46	31 VII 65	46–64	–
65–1506	Strait of Belle Isle	51 49	56 06	31 VII 65	70–99	–

FIG. 1. Stations of the *Calanus–Salvelinus* expeditions where athecate hydroids were collected.

gigantea, *Myriothela phrygia*, *Coryne hincksi* and *Rhizogeton nudus*. *Coryne pusilla*, *Sarsia tubulosa*, *Hydractinia monocarpa* and *Rhizorhagium roseum* occur in the North Pacific as well as subarctic and boreal regions of the Atlantic. *Clava multicornis* and *Eudendrium arbusculum* are Atlantic-boreal species, while *Sarsia eximia* and *Eudendrium vaginatum* are amphiboreal. *Hydractinia echinata*, *Eudendrium capillare*, and *E. tenellum* are wide-ranging species penetrating south of Cape Hatteras along the U.S. east coast. The geographic affinities of *Hydractinia laevispina*, a poorly known and poorly characterized species, and *Euphysa* sp., are uncertain.

The synonyms listed for each species are taken from literature pertaining to the immediate study area only, namely the waters extending northward from the coastline between the Strait of Belle Isle and the Alaska–Yukon border. Descriptions and illustrations have been made exclusively from specimens observed in the present collections. The distribution list for each species includes the recorded occurrence in cold waters of the northern hemisphere only. Records from the northern North Atlantic were derived mainly from Kramp (1943), those from the northern and far eastern seas of the USSR from Naumov (1960), and those of Alaska from Fraser (1937).

Systematic Account

Order Athecata (Gymnoblastea)
Suborder Capitata
Family Corymorphidae

Euphysa sp.

(Plate I, Fig. 1)

Collection record — Station 226.

Description — Polyps solitary, reaching 2 mm high, hydranths oval, 0.28–0.37 mm long, 0.15–0.22 mm wide in contracted specimens. Tentacles in two whorls, an oral whorl of 3–5 small capitate tentacles and an aboral whorl of 5–8 filiform tentacles. Hydranth base lacking backwardly directed papillae. Hydrocaulus covered with a loosely fitting, hyaline, wrinkled perisarc reaching nearly to the hydranth base. One specimen with two asexual bodies in the stolon, one of these having cytoplasmic contact with the parent polyp.

Medusa buds not seen.

Remarks — These specimens were similar in morphology to descriptions of *Corymorpha annulicornis* M. Sars 1859, a hydroid linked by Rees (1938) to the medusa *Euphysa aurata* Forbes 1848. They are therefore regarded as hydroids of *Euphysa*, but their specific identity remains doubtful. The hydranths lacked the basal papillae found on hydroids of *E. aurata* by Rees (1938) and others. The medusa of only one species of *Euphysa*, *E. flammea*, has been reported in northern Canada (Grainger 1959, 1965), but two others, *E. aurata* and *E. tentaculata*, are known from west Greenland (Kramp 1961).

Although this constitutes the first report of a hydroid of *Euphysa* in northern Canada, it is not the first record in North American waters. Rees (1957a) synonymized the hydroid *Dahlgrenella farcta*, described by Miles (1937) from the Mount Desert Island region of Maine, with *Euphysa*.

Rees (1946) showed that the family Hypolytidae, established by Fraser (1944) for *D. farcta* and *Hypolytus peregrinus*, was untenable. He noted that the characters upon which the family was based were insufficient even for species separation. However, Rees (1957a) recognized that the simple corymorphines *Hypolytus*, *Euphysa*, and possibly *Gymnogonos* were sufficiently distinct to warrant re-establishing Haeckel's (1879) subfamily Euphysinae.

Rees (1938) noted that the hydroid of *Euphysa aurata* has been recorded infrequently since it lives on mud substrates, and special methods are generally necessary for its collection. Hydroids of *Euphysa* examined here were found on such substrates as bryozoans and polychaete tubes.

Corymorpha groenlandica (Allman 1876)

(Plate I, Fig. 2)

Collection record — Station 62–002.

Description — Hydroid solitary, 5.5 cm long, base bulbous, 4.5 mm wide, with numerous rhizoids, remainder of the hydrocaulus cylindrical, 2 mm wide. Hydranth nearly 1 cm long, base broad. Aboral tentacles filiform, about 40 in number, reaching 1.5 cm long, oral tentacles numerous, scattered, filiform, reaching 4 mm in length, forming a tuft on the distal end of the hydranth.

Male gonophores oval, cryptomedusoid, borne on about 40 unbranched blastostyles reaching 5 mm long and arising just distal to the aboral tentacles. Female gonophores not seen.

Remarks — This record is based on a single specimen collected in Liverpool Bay. *C. groenlandica* is previously unreported in North American waters, although *Rhizonema carnea*, described by Clark (1876) from Alaska, may be a synonym. There is little in Clark's description of *R. carnea* to distinguish it from *C. groenlandica* other than the report of two types of aboral tentacles. The inner whorl of branched tentacles mentioned by Clark were probably blastostyles.

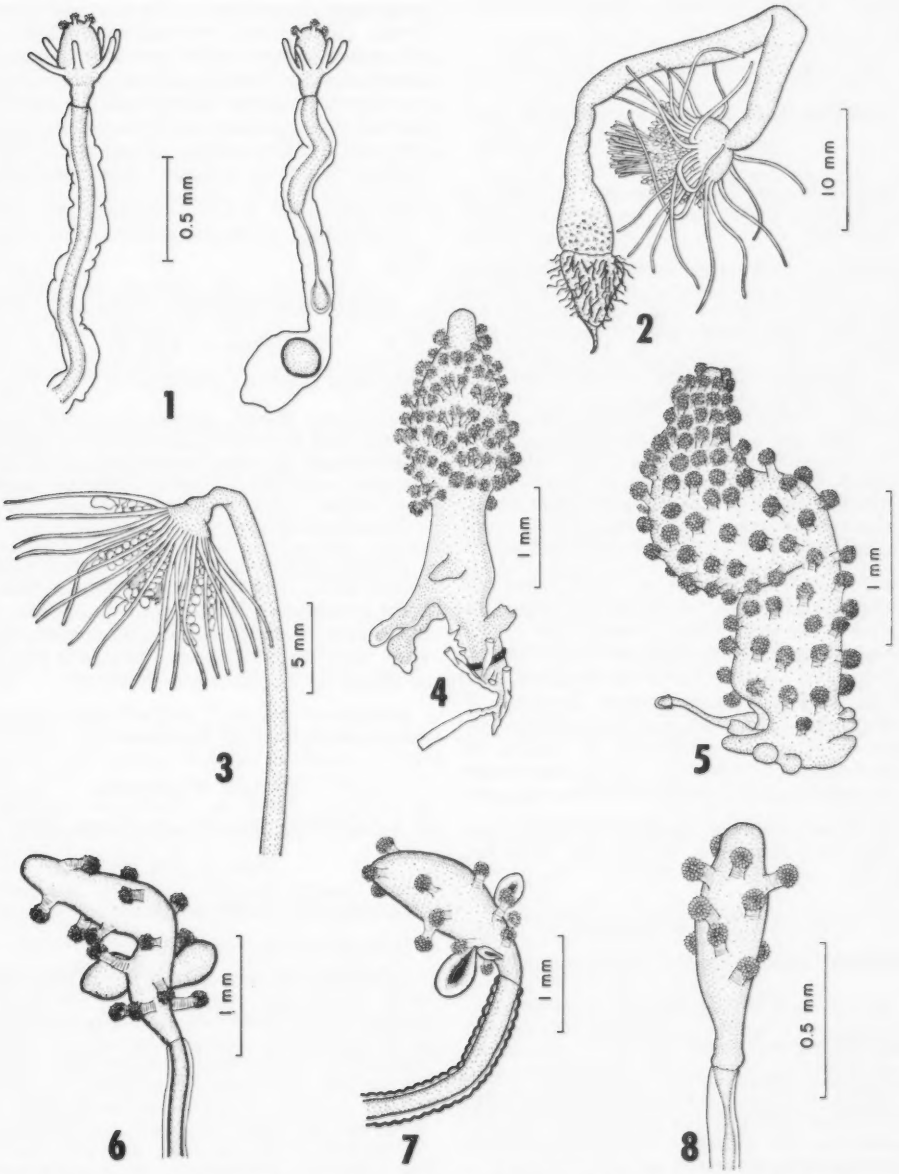

PLATE I. Fig. 1. *Euphysa* sp., sta. 226; Fig. 2. *Corymorpha groenlandica*, sta. 62–002; Fig. 3. *Tubularia regalis*, Herschel Island, N.W.T.; Fig. 4. *Monocoryne gigantea*, sta. 226; Fig. 5. *Myriothela phrygia*, sta. 226; Fig. 6. *Coryne hincksi*, sta. 59–29; Fig. 7. *C. pusilla*, sta. 61–43; Fig. 8. *Sarsia tubulosa*, sta. 203.

Distribution — Northern Canada (new record), west Greenland, Iceland, Spitzbergen, Barents Sea, Laptev Sea.

FAMILY TUBULARIIDAE

Tubularia regalis Boeck 1860

(Plate I, Fig. 3)

Collection record — N.M.C. collection, south of Herschel Island, 4–6 m, August 11, 1960, collector D. E. McAllister.

Description — Hydrocaulus unbranched, fragmentary in all specimens, longest measuring 5 cm, nearly uniform in diameter, reaching 1.5 mm wide, perisarc thick, smooth. Hydranth reaching 5.6 mm in length from basal constriction to tip of oral tentacles. Tentacles filiform, 25–45 in an aboral whorl, these reaching 12 mm long, oral tentacles short, numerous.

Gonophores borne on about 10 unbranched blastostyles arising just above the aboral tentacles, those bearing male gonophores reaching 6 mm long. Male gonophores cryptomedusoid, oval or nearly round, 0.6 mm long, 0.53 mm wide, spadix large. Female gonophores eumedusoid, 1.5 mm long, 0.9 mm wide, with about 4–8 laterally compressed longitudinal ribs.

Reamrks — Specimens of *T. regalis* resemble *T. indivisa*, and the two may be synonymous (Naumov 1960). *T. regalis* was recognized as a valid species by Broch (1916), who noted that the external longitudinal ribs on the female gonophores of *T. regalis* are absent on those of *T. indivisa*. *T. borealis*, briefly described by Clark (1876) from Alaska, is apparently similar to *T. regalis*, but Clark's characterization of his species was meagre and the species has not subsequently been recorded.

Distribution — Northern Canada (new record), west, east Greenland, Spitzbergen, Barents Sea, White Sea, Kara Sea.

FAMILY MYRIOTHELIDAE

Monocoryne gigantea (Bonnevie 1898)

(Plate I, Fig. 4)

Collection record — Station 226.

Description — Polyps solitary, contracted, 2.0–3.3 mm long, 0.55–1.5 mm wide, covered proximally with perisarc, basal anchoring filaments present. Tentacles numerous, scattered, capitate, trifid, with a large central branch flanked by two smaller branches.

Gonophores not seen.

Remarks — Rees (1956a) studied this species in detail and erected a new subfamily, the Monocoryninae, for the genus *Monocoryne* Broch 1910. Rees (1957b) synonymized the genus *Symplectanea* Fraser 1941 with *Monocoryne* after comparing *Symplectanea bracteata*, described by Fraser (1941) from Stevens Pass, Alaska, with *M. gigantea*. Fraser's family Symplectaneidae was also dropped by Rees since its characteristics placed it in the Myriothelidae. *M. bracteata* was provisionally retained as a separate species because of its large size and greater number of capitate heads per tentacle, but Rees suggested that more material might show it to be synonymous with *M. gigantea*.

Distribution — Northern Canada (new record), Barents Sea.

Myriothela phrygia (Fabricius 1780)

(Plate I, Fig. 5)

Collection record — Station 226.

Description — Polyps vermiform, contracted, 2.3–2.9 mm long, 0.8–1.0 mm wide, perisarc present only at the tips of the anchoring filaments. Tentacles unbranched, scattered, capitate, numerous, occurring nearly to the base of the polyp.

Gonophores not seen.

Remarks — This species differs from the closely related *Arum cocksi* in lacking perisarc over the basal portion of the polyp (Rees 1956a). Rees retained the well-established generic name *Myriothela* for this species, but recognized that it is antedated by the name *Candelabrum*.

Distribution — Northern Canada (new record), west Greenland, Barents Sea, Kara Sea.

FAMILY CORYNIDAE

Coryne hincksi Bonnevie 1898

(Plate I, Fig. 6)

Coryne brevicornis Broch 1907 p. 5.

Collection records — Stations 59–29, 65–1506.

Description — Colony reaching 2 cm high, perisarc thick, occasionally corrugated but not annulated. Branches few, irregularly placed, passing upward nearly parallel to the hydrocaulus, hydrocaulus and branches similar in size, about 0.25–0.30 mm wide. Hydranth elongate-oval when extended, reaching 2.5 mm long, 0.5–1.0 mm wide, tentacles scattered, capitate, about 20 in number, terminal knobs 0.20–0.24 mm wide.

Gonophores sporosacs, borne on fairly long stalks just above the proximal-most tentacles, about 2–5 per hydranth, oval, 0.95–1.04 mm long, 0.70–0.75 mm wide when fully developed, spadix distinct, occasionally with visible radial canals and ring canal, tentacles absent.

Remarks — This species was reported in North America from Jones Sound by Broch (1907) as

C. brevicornis. Rees (1956a) placed *C. brevicornis* in synonymy with *C. hincksi* after comparing the types of both species.

Although Bonnevie (1898b) reported the large gonophores to have four radial canals, Rees (1956a) was unable to find a trace of them. A few large specimens examined here from Hudson Bay bore visible radial canals, thus confirming Bonnevie's description.

Distribution — Northern Canada, Spitzbergen, Barents Sea.

Coryne pusilla (Gaertner 1774)

(Plate I, Fig. 7)

Coryne vermicularis Fraser 1931 p. 480; 1944 p. 39 fig. 9.

Collection records — Stations 58, 226, 61–11, 61–43.

Description — Colony 1.5 cm high, perisarc thick, annulated or wrinkled throughout, brown. Branching irregular, branches and hydrocaulus similar, 0.25–0.42 mm wide. Hydranth variable in shape, typically elongate-oval, reaching 2 mm long, 1 mm wide, tentacles capitate, scattered, about 20 in number, terminal knobs 0.13–0.22 mm wide.

Gonophores sporosacs, arising just above the proximal-most tentacles on short stalks, oval, 0.43–0.62 mm long, 0.33–0.50 mm wide when fully developed, spadix distinct. Radial canals, ring canal, tentacles absent.

Remarks — Although *C. pusilla* is common in the eastern Atlantic (Broch 1916), the only previous record in the western Atlantic is Fraser's (1931) report of *C. vermicularis* from Port Burwell. *C. vermicularis* was shown by Broch (1916) to represent merely a phase in the movement of the polyp of *C. pusilla*.

Distribution — Northern Canada, Iceland, Faeroes, Barents Sea, Sea of Okhotsk, Sea of Japan, Bering Sea.

Sarsia tubulosa (M. Sars 1835)

(Plate I, Fig. 8)

Coryne mirabilis Packard 1867 p. 264; 1891 p. 369. *Syncoryne mirabilis* Whiteaves 1901 p. 19; Fraser 1944 p. 41 fig. 14.

Collection records — Stations 203, 210, 59–50.

Description — Species represented by a few small specimens reaching 3.5 mm high. Branches, when present, nearly perpendicular to the hydrocaulus, width of the hydrocaulus 0.09–0.13 mm. Perisarc distinct, thin, mostly smooth but with a few wrinkles or annulations, particularly near the base. Hydranth oval when contracted, largest specimens 0.8 mm long, 0.4 mm wide, tentacles about 15 in number, scattered, capitate.

Medusa buds not seen.

Remarks — The complicated taxonomic history of this species was reviewed by Russell (1953). Both hydroid and medusa stages of *S. tubulosa* have been reported from the east, west, and north coasts of Canada (Kramp 1961).

Distribution — Northern Canada, west, east Greenland, Iceland, Barents Sea, White Sea, Kara Sea, Laptev Sea, East Siberian Sea, Sea of Okhotsk, Sea of Japan, Bering Sea, Alaska.

Suborder Filifera

Family Clavidae

Rhizogeton nudus Broch 1910

(Plate II, Fig. 1)

Collection record — Station 229.

Description — Zooids apparently lacking a perisarcal sheath, 0.85 mm high, 0.18 mm wide, arising singly from a reticulate stolon and constricted basally. Hypostome short, nearly cylindrical. Tentacles filiform, about 12–15 in number, scattered over the distal two-thirds of the zooid.

Male gonophores oval in lateral view, round in cross-section, arising from the stolon network from a short pedicel and covered with thin, closely adhering perisarc. Female gonophores not seen.

Distribution — Northern Canada (new record), west, east Greenland, Spitzbergen, Barents Sea.

Family Hydractiniidae

Hydractinia carica Bergh 1887

(Plate II, Fig. 2)

Hydractinia carica Fraser 1931 p. 480; 1944 p. 77 fig. 53; Rees 1956c p. 355 fig. 1, 2.

Collection record — Station 901.

Description — Gastrozooids reaching 2.5 mm high in expanded specimens, cylindrical with expanded hydranths (one zooid with two hydranths), arising singly from an encrusting base. Manubrium elongate, tentacles filiform, in one whorl, 8–15 in number. Spines fairly numerous, up to 0.35 mm high, conical, smooth, horn-coloured. Gonozooids not seen.

Remarks — As Broch (1916) and Rees (1956c) have noted, *Hydractinia minuta* Bonnevie 1898 is a synonym of *H. carica*.

Distribution — Northern Canada, Spitzbergen, Barents Sea, White Sea, Kara Sea, Sea of Okhotsk, Sea of Japan, Chukchi Sea, Bering Sea.

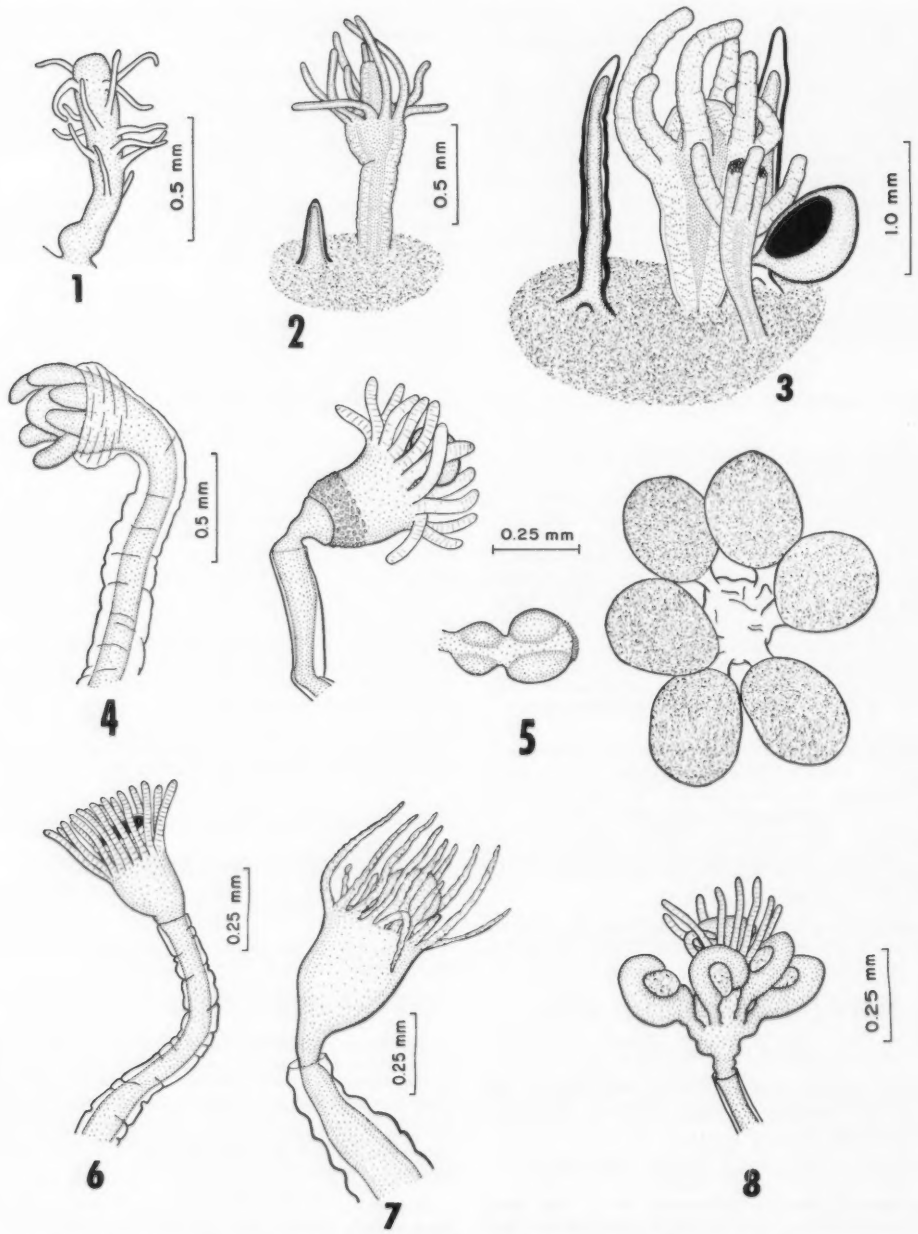

PLATE II. Fig. 1. *Rhizogeton nudus*, sta. 229; Fig. 2. *Hydractinia carica*, sta. 901; Fig. 3. *H. monocarpa*, sta. 65–1505; Fig. 4. *Rhizorhagium roseum*, sta. 59–64; Fig. 5. *Eudendrium arbusculum*, hydranth, sta. 58; male gonophore, sta. 58; developing planulae, sta. 61–26; Fig. 6. *E. capillare*, sta. 58; Fig. 7. *E. rameum*, sta. 201C; Fig. 8. *E. tenellum*, hydranth with female gonophores, sta. 61–26.

Hydractinia monocarpa Allman 1874

(Plate II, Fig. 3)

Collection record — Station 65–1505.

Description — Gastrozooids club-shaped, reaching 1 mm high (specimens contracted), arising singly from an encrusting base. Tentacles filiform, in one whorl, 5–8 in number, manubrium typically dome-shaped. Spines numerous, 0.7–1.0 mm long, cylindrical, hollow, wrinkled slightly, but not jagged, tip round or pointed. Gonozooids cylindrical, 0.7 mm high, 2–5 filiform tentacles and 1–4 gonophores per zooid, occasional zooid almost atrophied and bearing a single gonophore.

Remarks — This record is based on a single colony growing on the stem of a sertularian. According to Naumov (1960), *H. monocarpa* is fairly common on gastropod shells in the northern seas of the USSR.

Distribution — Northern Canada (new record), west Greenland, Spitzbergen, Barents Sea, White Sea, Kara Sea, Laptev Sea, Sea of Okhotsk, Bering Sea.

Family Bougainvilliidae

Rhizorhagium roseum M. Sars 1877

(Plate II, Fig. 4)

Garveia groenlandica Fraser 1931 p. 480; 1944 p. 56 fig. 27.

Collection record — Station 59–64.

Description — Hydrocaulus unbranched, 1.1 mm high, 0.12 mm wide, perisarc of moderate thickness, wrinkled throughout, hydranth base covered by a conspicuous pseudohydrotheca. Hydranth drooping, about 0.25 mm long, 0.20 mm wide, tentacles filiform, in a single whorl, 8 in number.
Gonophores not seen.

Remarks — This record is based on a single, small, sterile specimen. The hydroid was compared with well-developed, fertile colonies of *R. roseum* in the Museum of Natural Sciences from the Saguenay River, Quebec, and is regarded as the same species.

Several authors, including Broch (1916), Kramp (1932a, b, 1943) and Naumov (1960) followed Bonnevie (1898a) in placing this species in the genus *Perigonimus*. Rees (1938) showed that *Perigonimus* is untenable as a generic name because its type species, *P. muscoides*, is a *Bougainvillia*. In a revision of the genus, Rees (1956b) found that hydroids of *Perigonimus* are referable to at least 10 genera encompassing three orders. Rees (1938, 1956b) recognized Sars' (1877) genus *Rhizorhagium* for *R. roseum*.

Broch (1916) demonstrated that *Garveia groenlandica* is a synonym of *R. roseum*.

Distribution — Northern Canada, west, east Greenland, Barents Sea, White Sea, Alaska.

Eudendrium arbusculum Wright 1859

(Plate II, Fig. 5)

Eudendrium caricum Kramp 1932b p. 19 fig. 8.

Collection records — Stations 58, 61–26.

Description — Colonies reaching 4.5 cm high, hydrocaulus and main branches polysiphonic, branches either annulated throughout or with some smooth portions, branching irregular, perisarc thick. Hydranths about 0.5–0.6 mm long, with a band of large nematocysts just above a basal annular incision. Tentacles filiform, in a single whorl, about 20 in number.

Male gonophores borne on atrophied hydranths, two-chambered, distal end with a conspicuous pad of nematocysts. Branchlets bearing female gonophores short, usually annulated or wrinkled throughout, hydranths on these branchlets reduced or completely atrophied, branchlets often terminating in a knob lacking a distal opening. Female gonophores oval, spadix unbranched, curving over the ovum. Ova frequently borne part-way down the branchlets and connected with the coenosarc by a cytoplasmic connection.

Remarks — Originally described by Jäderholm (1908) from the Russian Polar Expedition collections, *Eudendrium caricum* was placed in synonymy with *E. rameum* by Kramp (1911) in studies on Greenland hydroids. Later, Kramp (1932b) reinstated *E. caricum* as a valid species after examining material from Davis Strait and Smith Sound. Specimens of *E. arbusculum* examined here encompassed the characteristics of *E. caricum* in their morphology, and the two are considered synonymous. *E. arbusculum* is marked by a band of large nematocysts about the proximal portion of the hydranth. Hydranths were lacking in Kramp's specimens.

In the hydroids examined by Kramp (1932b), gonophores were borne on short, irregularly wrinkled branchlets terminating in a rounded knob having no distal opening. Gonophores were situated laterally on the branches and were either scattered or arranged in a whorl. Specimens of *E. arbusculum* from the *Calanus* collections conformed to Kramp's description, but branchlets bearing gonophores occasionally terminated in reduced hydranths also bearing gonophores. Presence of ova part-way down on the branchlets in *E. arbusculum* was explained by Hamond (1957). He observed that a hydranth may regress after forming ova, and that a new hydranth may subsequently develop, ac-

companied by an elongation of the hydrocaulus. Thus, the ova are left on the branchlet below the base of the new hydranth. The latter may then produce a new series of ova.

Broch (1916) regarded *E. arbusculum* as a southern, littoral species capable of penetrating into northern waters. Along the European coast, *E. arbusculum* has been recorded from the Mediterranean Sea northward to the Trondheimfjord, Norway (Broch 1916; Vervoort 1946).

Distribution — Northern Canada, west Greenland, Faeroes, Kara Sea.

Eudendrium capillare Alder 1856

(Plate II, Fig. 6)

Collection records — Stations 28, 58, 226, 616, 61–24.

Description — Colony small, delicate, 2.5 cm high, hydrocaulus monosiphonic, reaching 0.15 mm wide. Branches numerous, irregularly placed, rebranched. Perisarc moderately thick, annulated at the base of the hydrocaulus and branches, on the hydrocaulus above the branches, and occasionally elsewhere. Hydranths about 0.3 mm long, tentacles filiform, in a single whorl, about 20 in number.

Gonophores not seen.

Remarks — Although *E. capillare* is a widespread species, it does not penetrate very far into arctic waters (Broch 1916).

Distribution — Northern Canada (new record), west Greenland, Iceland, Faeroes, Spitzbergen, Barents Sea, White Sea, Sea of Okhotsk, Sea of Japan, Bering Sea, Alaska.

Eudendrium rameum (Pallas 1766)

(Plate II, Fig. 7)

Eudendrium rameum Fraser 1931 p. 480; Kramp 1932b p. 18; Fraser 1944 p. 71 fig. 47.

Collection records — Stations 201C, 811, 59–29.

Description — Colony bushy, 6 cm high, hydrocaulus and main branches polysiphonic, branches numerous, irregularly placed, usually arising from the parent branch at an angle of 45 degrees or less. Perisarc fairly thick, horn-coloured, annulated at the base of the branches, occasionally elsewhere but smooth for the most part. Hydranths about 0.6 mm long, in poor condition, tentacles filiform, in one whorl, number indeterminable.

Gonophores not seen.

Distribution — Northern Canada, west, east Greenland, Iceland, Faeroes, Spitzbergen, Barents Sea, White Sea, Kara Sea, Laptev Sea, East Siberian Sea, Sea of Okhotsk, Sea of Japan, Bering Sea, Alaska.

Eudendrium tenellum Allman 1877

(Plate II, Fig. 8)

Eudendrium tenellum Fraser 1922 p. 4; 1931 p. 480; 1944 p. 74 fig. 50.

Collection records — Stations 58, 103, 225, 406, 547, 616, 61–26, 62–4001, 65–1048.

Description — Colony small, reaching 7 mm high, hydrocaulus monosiphonic, up to 0.13 mm wide, branches few, irregularly placed. Perisarc fairly thin, light or dark brown, annulated at the base of the hydrocaulus and branches, scattered annulations elsewhere. Hydranths with about 18–20 filiform tentacles in a single whorl.

Gonophores borne around the base of entire hydranths, male gonophores oval, one-chambered, 0.20 mm long, 0.18 mm wide, female gonophores with an unbranched spadix curving over the egg.

Remarks — *E. tenellum* is similar to *E. capillare*, and the two species were considered synonymous by Naumov (1960). *E. tenellum* is usually distinguished from *E. capillare* by its smaller colony size, by being much less branched, and by having gonophores on entire rather than on atrophied hydranths.

Distribution — Northern Canada, west, east Greenland, Spitzbergen, Barents Sea, northern seas of the USSR(?), Alaska.

Additional Records

A number of species recorded from the study area by previous investigators were not identified in the examined collections. These species, and their collection locations, are given below. This list does not include records of specimens from depths exceeding 300 m.

Family Corynidae

Sarsia eximia (Allman 1859). Richmond Gulf (Fraser 1922 p. 4; 1931 p. 480; 1944 p. 40 fig. 13: as *Syncoryne eximia*). In Canadian waters the medusa of this species is known only from the Pacific coast (Kramp 1961).

Family Clavidae

Clava multicornis (Forsklå 1775). Labrador (Packard 1863 p. 404; 1867 p. 264; 1891 p. 369; Whiteaves 1901 p. 18; Fraser 1944 p. 33 fig. 1: as *C. leptostyla*).

Family Hydractiniidae

Hydractinia echinata (Fleming 1828). Labrador (Packard 1863 p. 404, 422; 1867 p. 263; 1891 p. 369: as *H. polyclina*. Fraser 1944 p. 78 fig. 55).

Hydractinia laevispina Fraser 1922. Bernard Harbour, N.W.T. (Fraser 1922 p. 4).

Family Eudendriidae

Eudendrium vaginatum Allman 1863. Hudson Strait (Fraser 1931 p. 480; 1944 p. 76 fig. 52).

Acknowledgments

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Effects of Volcanic Ashfalls on Chemical and Sediment Characteristics of Two Alaskan Lakes[1]

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BARSDATE, R. J., AND R. C. DUGDALE. 1972. Effects of volcanic ashfalls on chemical and sediment characteristics of two Alaskan lakes. J. Fish. Res. Bd. Canada 29: 229–236.

Cores from two lakes on Afognak Island, 150 km southeast of the Aleutian volcanic arc, indicated that several ashfalls have formed continuous layers over the lake basins, at least partially returning the lakes to a juvenile state with respect to their sediments. Abundant diatom remains were found in the sediments above each ash layer. During several hundred years after each ashfall, the transition to mature conditions followed a pattern characterized by decreasing diatom abundance and gradual increases in organic matter and clay-size inorganic particulates. High silica concentrations occurred in lakes within the area covered by the ashfall of the 1912 Mount Katmai eruption.

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Des carottes prélevées dans deux lacs de l'île Afognak, à 150 km au sud-est de l'arc volcanique des Aléoutiennes, révèlent que plusieurs retombées de cendres ont recouvert de couches continues le bassin de ces lacs, rétablissant, du moins partiellement, leurs sédiments à un stade juvénile. Des restes abondants de diatomées ont été trouvés dans les sédiments au-dessus de chaque couche de cendres. Pendant plusieurs centaines d'années après chaque retombée de cendres, le passage au stade mûr est caractérisé par une diminution des diatomées et une augmentation graduelle de matière organique et de particulats inorganiques de la grosseur de l'argile. De fortes concentrations de silice ont été observées dans les lacs de la zone affectée par la retombée de cendres qui a suivi l'éruption du mont Katmai en 1912.

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THE work reported here is an attempt to determine the effects of ashfalls on two Alaskan lakes, primarily through an examination of the sedimentary record. We have analyzed lake bottom deposits chemically for organic carbon, nitrogen, and phosphorus, and mechanically for clay, silt-size, and larger inorganic particles (clastics), and the siliceous remains of diatoms. The results were evaluated to determine the nature and extent of changes in sediment composition following ashfalls, and to determine the approximate time scale involved in the reestablishment of mature, pre-ashfall sediment conditions (particularly to determine if the modern lake sediments were still under the influence of the 1912 Katmai ashfall). These data, and information from various sources on other southwest Alaskan lakes, were examined for indications of change in chemistry and fertility resulting from volcanic ashfalls.

The mechanical separation of a lake from its former sediments by a cohesive layer of ash would affect, presumably unfavorably, the habitat of bottom-dwelling organisms, and reduce the rate of diffusion of remineralized nutrients from the pre-volcanic sediments. Goldman (1960) found that small quantities of sediment extract greatly increased the primary productivity of the plankton in Brooks Lake on the Alaska Peninsula. However, volcanic ash lay-

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ers on the watersheds contribute to the ionic components of surface waters, and perhaps indirectly influence runoff composition by altering the pattern of water flow through the soil horizons. Major ashfalls, such as that accompanying the 1912 Mount Katmai eruption (Fig. 1), have deposited sufficient pyroclastic materials to profoundly influence the terrestrial flora and to isolate the lakes from their pre-eruption sediments.

The study lakes, Upper Jennifer and Little Kitoi, are on Afognak Island (20 miles north of the city of Kodiak) near the Kitoi Bay Research Station of the Alaska Department of Fish and Game. They are close together and have nearly identical surface areas, mean depths, and thermal regimes (Wallace MS 1959), along with similar phosphorus budgets (Dugdale and Dugdale 1961). Upper Jennifer Lake has a restricted watershed in glacial ground moraine, and Little Kitoi Lake has a relatively large watershed with areas of high relief.

Methods

Cores were obtained from both lakes at depths of approximately 25 m (the maximum depth of Little Kitoi is 28 m; Upper Jennifer, 29 m). Post-Katmai sediments were sampled with a core freezer (Shapiro 1958). With this device, the thin flocculent material above the Katmai ash was frozen in place at the lake bottom, brought quickly to the surface, and kept frozen until sectioned in the laboratory. Additional longer cores, about 0.5 m, were obtained at the same depths by divers using simple 5-cm diameter coring tubes equipped with ball-check valves. These were brought to the surface, frozen, extracted from the tubes with a hydraulic jack, and maintained in a frozen state.

The frozen cores were cut lengthwise on a jigsaw, and the cut surfaces partially polished, photographed, and then sectioned in nominal 1-cm intervals. Some deformation of the sediments occurred either during the coring operation or in the subsequent freezing of the core material. In order to minimize the effects of deformation, sections were cut along the boundary be-

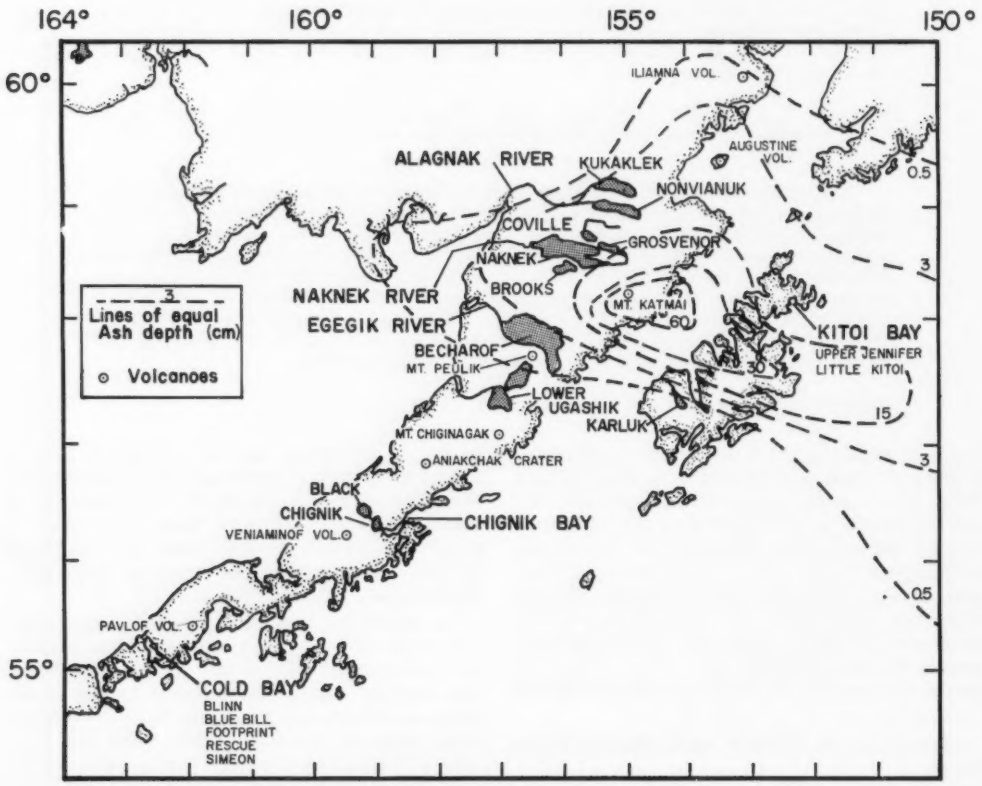

FIG. 1. Alaska Peninsula showing distribution of ashfall from 1912 Mt. Katmai eruption (after Wilcox 1959).

tween layers of differing color, texture, or both. In areas with no indications of deformation, the sections were cut normal to the length of the core. Sections of the core material for *p*H determinations were thawed and centrifuged, and the measurements made promptly in the centrifuge tubes. Material for other determinations was dried at 100 C, and kept in a desiccator over anhydrous magnesium sulfate.

Total carbon analyses were performed with a Coleman Automated Nitrogen Analyzer, modified for micro-Pregl carbon technique. Volumetric determinations for carbon dioxide liberated from core material upon treatment with dilute hydrochloric acid were made; no carbonate-carbon was found within the limit of sensitivity of the method (approximately 0.2% $CaCO_3$ by weight). Total nitrogen determinations (micro-Dumas) were made with a Coleman Nitrogen Analyzer.

Phosphorus was determined colorimetrically by a modification of the method of Fiske and Subbarow (1925), following perchloric acid digestion. The determination was nearly quantitative for organic phosphorus, but the digestion did not quantitatively extract phosphorus from the crystal lattice of minerals, or from volcanic glass.

Determinations of inorganic particulate material were made after removal of the organic fraction of the sediments with 30% hydrogen peroxide, 0.05 M in H_2SO_4. A weighed portion of the residue was centrifuged and washed with distilled water, and the clay-size fraction was separated by differential sedimentation, dried, and weighed. The determination was crude, the standard deviation being about ±10%. The remainder of the residue, consisting of particles silt-size and larger, was dried, immersed in cedar oil, examined with a petrographic microscope, and classified as diatom remains or as clastics (volcanic glass shards and mineral grains). Seven or more fields, containing from 20 to 200 classifiable objects each, were observed. With the use of a grid ocular, the long axis and right-angle intercept of each object were measured, and the object's area was calculated. The diatom and clastic fractions were estimated by assuming that the weight of the particles was directly proportional to the area as measured. The organic fraction was assumed to be 2.5 times the organic carbon concentration.

Primary productivity was measured on the lakes with the ^{14}C method of Steemann Nielson (1952). Results of 24-hr vertical series in situ were integrated to obtain the rate of carbon fixation/unit surface area.

Results

The bottom deposits of Upper Jennifer Lake consist of about 0.7 cm of loose flocculent sediment, 8 cm of Katmai ash, and 28 cm of pre-Katmai organic sediment interrupted by several ash layers (Fig. 2). The sediment sequence in Little Kitoi Lake has about 1.1 cm of loose surface material, 10 cm of Katmai ash, and 36 cm of pre-Katmai sediment terminating in 10 cm of sharp pebbles underlain by apparently terrestrial peat.

In Little Kitoi Lake, the dark red ash (no. 8, Fig. 2) is 10 cm below the base of the Katmai ash, in comparison with 6 cm in Upper Jennifer Lake (no. 3, Fig. 2). Therefore the sedimentation rate in Upper Jennifer Lake was 60% of that in Little Kitoi Lake in pre-Katmai time. The post-Katmai sedimentation has approximately the same ratio: 0.7 cm in Upper Jennifer Lake vs. 1.1 cm in Little Kitoi Lake (or 62%).

The organic carbon content increases above each ash layer (Fig. 2) to a steady state of 8–10% of the dry weight of the total sediment 2–3 cm above the ash. The rate of recovery is not influenced greatly by the thickness of the ash layers. Several thin, poorly defined layers containing appreciable pyroclastic material occur, but their carbon content remains relatively constant. The increase of organic carbon to the steady state occurs over a slightly greater length of core in Little Kitoi Lake than in Upper Jennifer Lake, but because of the greater rate of sedimentation in Little Kitoi Lake, the times involved are probably similar for the two lakes.

Nitrogen content varies with organic carbon (Table 1), producing a mean C/N ratio of 10.7 in Little Kitoi Lake, and 11.1 in Upper Jennifer Lake for those sediments containing 8% or more carbon (assumed steady state). The difference in these ratios is not significant; however, the variability of the C/N ratio is greater in Little Kitoi Lake than in Upper Jennifer Lake (standard deviation of ± 0.5 vs. ± 0.1). In the less carbonaceous sediments the C/N ratio varies unsystematically but more widely, the extremes being 4.8 and 16.2. At least part of the increased variation can be attributed to less precision in the analytical techniques for small amounts of carbon and nitrogen. Since C/N ratios are high in terrestrial vegetation, Little Kitoi Lake, with its low rate of plankton primary productivity, large watershed, and high sedimentation rate, would be expected to display a higher C/N ratio than would Upper Jennifer Lake. The similar and rather low C/N ratios in the two lakes suggest that allochthonous organic detritus is a rather minor component of the sediments, a situation which is difficult to accept in relation to their oligotrophic character.

The phosphorus concentration in the sediments varies from 0.01 to 0.21% (Table 1). The C/P ratios vary from < 5 to 87, being lowest in the ash layers and highest in the steady state. Analyses of the Katmai ash in our study range from 0.01 to 0.02% P, but Griggs (1920) noted that the phosphorus content of a composite sample of Katmai ash was 0.36% P_2O_5 (0.16% P). It should be emphasized here that the perchloric acid digestion used in the phosphorus method we employed is not quantitative for volcanic ash minerals, and no loss of P from the lake bottom

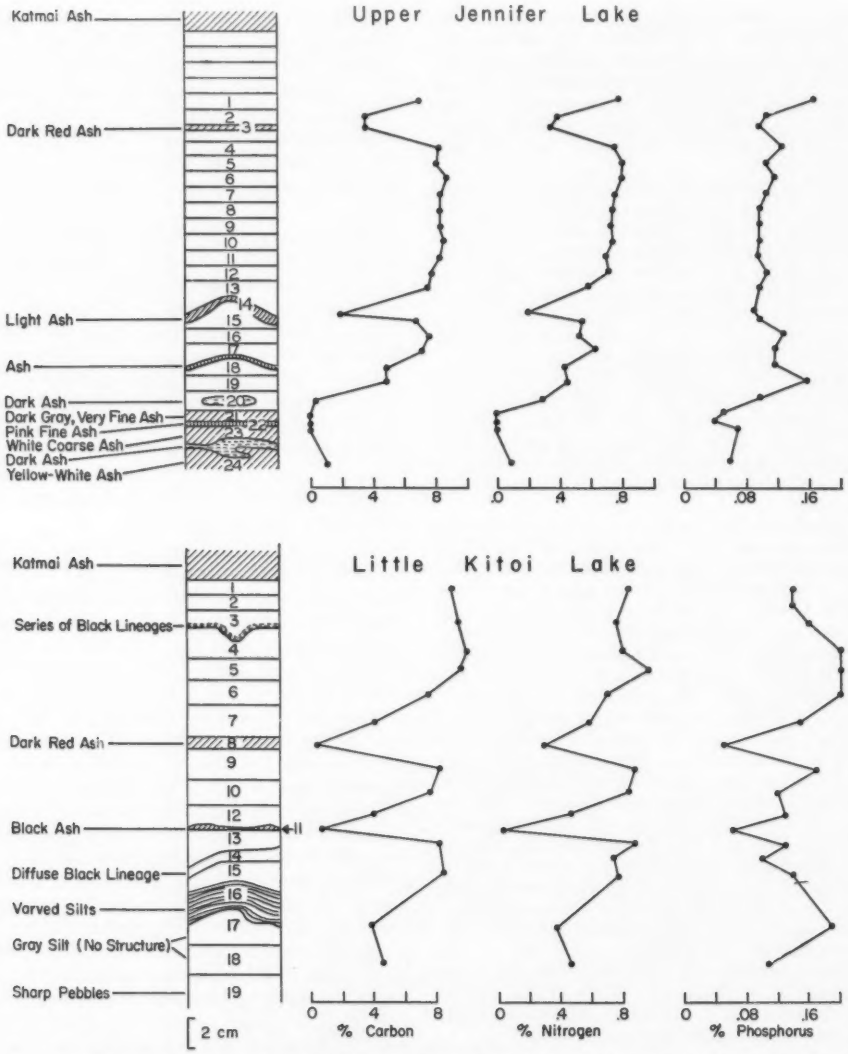

FIG. 2. Core sketches and chemical determinations by weight of sediments in the study lakes.

ash is implied in the comparison with Griggs' data. The phosphorus concentration in the organic sediments tends to be higher and somewhat more variable in Little Kitoi Lake than in Upper Jennifer Lake. The mean C/P ratio for steady state conditions is 56 in Little Kitoi, and 81 in Upper Jennifer. The sediment–phosphorus concentration, which is higher in the less productive Little Kitoi Lake, is not a promising characteristic to correlate with changes in lacustrine productivity.

The clay content of the ash layers is low, ranging from <1% in the Katmai ash to about 10% in the thinner ash layers (Table 1, Fig. 3). Roughly paralleling the concentration of organic matter, the clay fraction increases rapidly above each ashfall, reaching 60–70%. Only in the ash layers are the silt-size and larger clastics the most abundant components. This material rapidly decreases in quantity above the ash, and forms about 1% of the sediment in the steady state. Diatoms are most abundant immediate-

TABLE 1. Sediment core composition, and carbon, nitrogen, and phosphorus concentrations at various distances above the prominent ash layers in the two lakes. Values in percent by weight for single determinations.

Distance above ash layer (*cm*)	Core layer[a]	Organics	Diatoms	Clastics	Clay	C	N	P	C/N	C/P
Upper Jennifer Lake					*Katmai ash*					
0.6		14	25	14	47	5.4	0.48	0.08	11.3	66
0.2		13	33	10	44	5.1	0.46	0.08	11.0	64
0.1		6	66	8	20	2.6	0.22	0.06	12.0	42
–0.5		1	2	92	5	0.3	0.02	0.02	15.0	20
					Dark red ash					
2.5		22	14	1	63	8.8	0.81	0.11	10.9	80
1.5	1	18	40	1	41	7.2	0.80	0.17	9.0	42
0.5	2	9	69	3	19	3.8	0.40	0.11	9.5	34
–0.2	3	9	1	80	10	3.7	0.36	0.10	10.3	37
					Light ash					
3.5	11	21	11	1	67	8.5	0.71	0.10	11.9	85
2.5	12	20	14	2	64	7.9	0.73	0.11	10.8	74
1.0	13	19	15	2	64	7.7	0.60	0.10	12.9	76
0.0	14	5	48	37	10	2.0	0.21	0.09	9.5	23
Little Kitoi Lake					*Katmai ash*					
0.8		17	20	15	48	6.6	0.62	0.10	10.7	69
0.2		9	20	41	30	3.6	0.41	0.08	8.8	44
–0.5		1	2	92	5	0.3	0.02	0.02	15.0	20
					Dark red ash					
4.3	5	24	9	1	66	9.6	0.97	0.20	9.9	49
2.8	6	19	17	2	62	7.5	0.70	0.20	10.7	38
1.0	7	10	34	8	48	4.1	0.59	0.15	7.0	28
–0.4	8	1	6	84	9	0.3	0.03	0.05	8.7	5

[a]Layer numbers from core sketches in Fig. 2.

ly above the ash layers, the concentration being higher in the sediments of Upper Jennifer Lake.

The *p*H of the interstitial water in the post-Katmai sediment and at the upper surface of the Katmai ash in both lakes is 7.5, approximately the same as the hypolimnia. The *p*H drops gradually to 7.1 at the middle of the ash, and increases to 7.7 at the lower ash–mud interface. Extreme *p*H conditions, which might affect sedimentary processes, were not found in association with the Katmai ash.

The rate of photosynthetic carbon fixation, as measured by the ^{14}C method, was invariably higher in Upper Jennifer Lake than in Little Kitoi Lake. During the period of investigation, the mean primary productivity of Upper Jennifer Lake was 70% more than that of Little Kitoi Lake. The values (mg C fixed/m^2 per day) on six occasions from late May to mid-July were:

	May		June			July	Mean
	22	27	3	19	30	13	
Upper Jennifer	154	160	268	214	462	369	271
Little Kitoi	86	130	155	69	241	273	159

Discussion

The role of fresh inorganic sediments in restricting the return of nutrients from previous deposits is well documented for productive lakes. Findenegg (1969) reported that the eutrophication of the Mondsee in the Austrian Alps was retarded by solids washed in from a strip-mining operation, and that temporary de-eutrophication of the highly polluted Zeller Sea in Salzburg followed the deposition of silt brought in by heavy floods. For oligotrophic lakes,

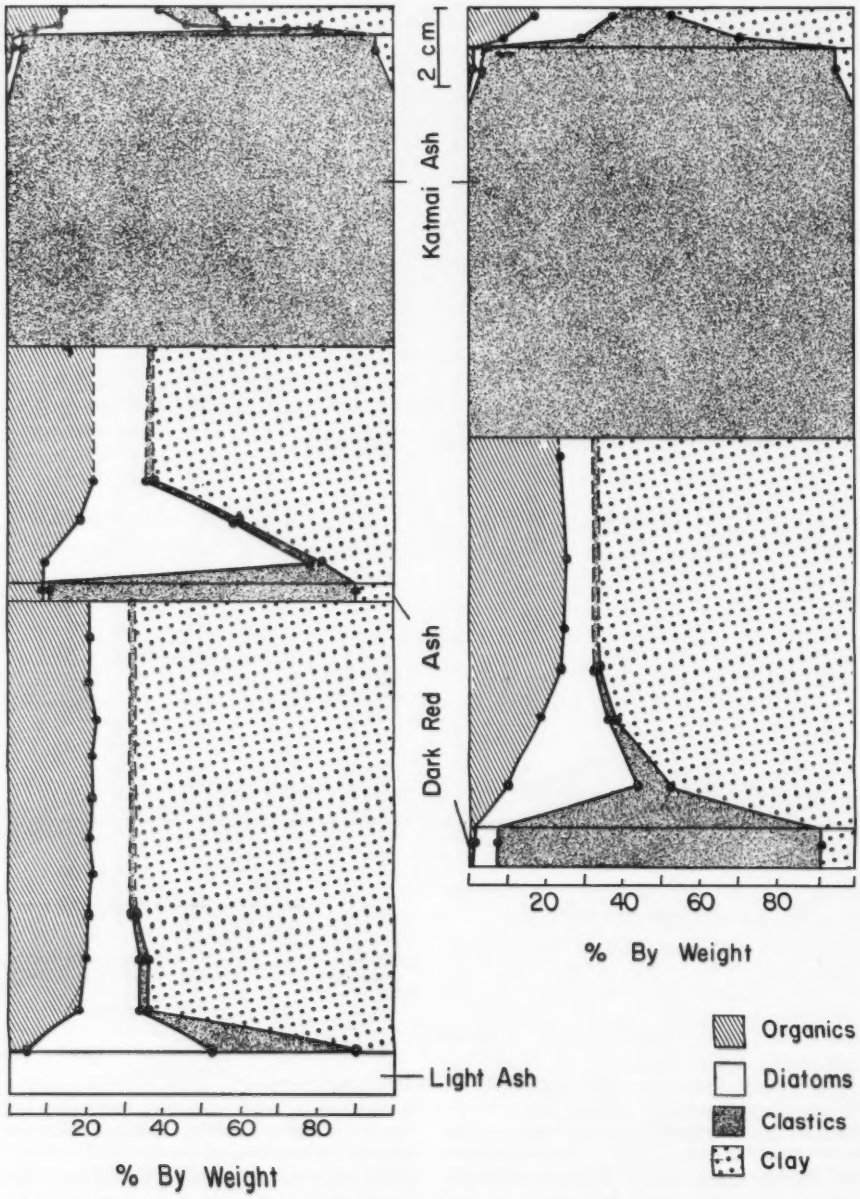

FIG. 3. Core profiles showing vertical distribution of organics, diatoms, clastics, and clay in Upper Jennifer (left) and Little Kitoi lake (right) sediments.

particularly the cold, relatively deep waters that have been investigated here, contributions from the sediments are relatively less important than in eutrophic lakes, and factors which influence the components of discharge from the watershed might be far more important in the regulation of fertility.

Griggs (1920), Eicher and Rounsefell (1957), and Parker and Vincent (1955) found that the growth of terrestrial vegetation accelerated several years after the Mount Katmai eruption, and continued at a rate higher than that preceding the eruption. Griggs had noted, however, that the acid volcanic ash of the Katmai eruption was nutrient poor, and he attributed the accelerated vegetative growth not to the addition of beneficial chemical factors, but to the mechanical effects of the ash. Shipley (1920) found very little combined nitrogen (as ammonia or nitrite) in the ash, and Goldman (1960) concluded that there is little reason to expect a stimulating effect on primary productivity from the type of ash associated with the Katmai eruption.

In respect to possible increase in primary and secondary production after volcanism, Eicher and Rounsefell (1957) summarize evidence for the theory that the Katmai ash has had a fertilizing effect on the lakes of the area, and speculate that intermittent volcanism may be significant in determining the abundance of red salmon, *Oncorhynchus nerka* (Walbaum).

The large amount of diatomaceous matter sedimented immediately following each major ashfall indicates either a major reduction in the rate of deposition of clay and organic matter, or an increase in the diatom productivity in the lakes. The latter alternative is favored by the findings of Kurenkov (1966), who reported the limnological effects of the 1956 eruptions of Mount Besymjanny in Kamchatka. Since the eruptions, the diatom population in Lake Asabatchye has risen from about 10^4 cells/liter to about 10^5 cells/liter, and the primary consumer (*Cyclops*), although seemingly depressed in numbers for 4 years after the eruptions, also has in-

TABLE 2. Silica concentrations and plankton primary productivity in lakes of Kodiak (K), Afognak (A), and the Alaska Peninsula (AP).

Lake	Region	H_4SiO_4–Si (*ppm*)	Primary Productivity[a] *mg* C/m³ per day	Primary Productivity[a] *mg* C/m² per day	Source
Lakes in areas of <3 cm recent ashfalls					
Becharof	Egegik River (AP)	1.0	0.6	–	Goldman 1960
Blinn	Cold Bay (AP)	0.04	4.4	–	Barsdate unpublished data
Blue Bill	Cold Bay (AP)	0.18	2.2	–	
Footprint	Cold Bay (AP)	0.19	19.0	–	
Rescue	Cold Bay (AP)	0.51	11.0	–	
Simeon	Cold Bay (AP)	0.01	6.2	–	
Lower Ugashik	Ugashik River (AP)	1.4	3.6	123	
Karluk	Karluk River (K)	0.4	17.7	393	
Average		0.46	8.1	258	
Lakes in areas of >5 cm recent ashfalls[b]					
Nanvianuk	Alagnak River (AP)	4.1	3.6	72	Burgner et al. 1969
Kukaklek	Alagnak River (AP)	1.1	3.3	66	
Brooks	Naknek River (AP)	10.5	5.1	141	
Coville	Naknek River (AP)	9.0	17.7	297	
Grosvenor	Naknek River (AP)	7.7	8.7	183	
Naknek	Naknek River (AP)	9.3	10.2	177	
Black	Chignik Bay (AP)	12.9	100.2	363	
Chignik	Chignik Bay (AP)	12.6	40.5	774	
Little Kitoi	Kitoi Bay (A)	7.3	9.9	159	This paper
Upper Jennifer	Kitoi Bay (A)	4.9	19.4	271	This paper
Average		7.9	21.9	250	

[a]Primary productivity data from Burgner et al. (1969) have been converted from 4-hr rates to daily rates by tripling the values.

[b]Black and Chignik Lakes are in the area of ashfall from recent eruptions of Mt. Veniaminof (Wilcox 1969; Coats 1950; Knappen 1929); all other lakes listed are in the area of ashfall from the 1912 Mt. Katmai eruption.

creased tenfold over the pre-eruption years. The sustained increase in numbers of diatoms and *Cyclops* may not have been caused exclusively by the 1956 Besymjanny ashfalls, for minor volcanism has occurred since.

A characteristic progression occurs in Upper Jennifer and Little Kitoi lakes following major ashfalls. On the bases of high diatom abundance, low organic carbon concentration, and the small thickness of accumulated post-Katmai sediments, it is apparent that these lakes are still within the recovery period following the Katmai ashfall. The present diatom abundance in these lakes suggests an increase in silica supply over pre-eruption levels. If the period of silica enrichment is in fact reflected in the increase in diatom remains in the lakes of this study, an estimate of the time scale involved can be obtained. The post-Katmai sedimentation rate in Little Kito iLake is approximately 2 cm/century, and an increased diatom content is evident for about 3.5 cm above a pre-Katmai ash layer in this lake (Fig. 3). While compaction of the sediments and upward mixing of diatomaceous material by the benthos prevent a linear extrapolation of time from sediment accumulation, the processes resulting in the higher diatom abundance evidently are active for at least 100 years, and perhaps several times that. The ultimate decline in silica may be a result of depletion of relatively soluble silicate minerals in the watershed, but it is more probable that the vegetative mat and soil formed over the ash eventually reduces the effectiveness of leaching by runoff water.

In order to determine if high silica and productivity are associated with major recent ashfalls in southwestern Alaska, the existing information for lakes of this area has been reviewed and compiled. On the basis of the data of Wilcox (1959), Coats (1950), Knappen (1929), and our field observations, the lakes have been divided into two categories: those receiving < 3 cm of ash and those receiving > 5 cm. The striking difference in the silica content of the water of the groups (Table 2) leaves little doubt concerning the role of ashfalls in the supply of silica. However, the productivity data display a much weaker relation to ash thickness. It is not surprising that a massive response would not occur, as these lakes are nutrient poor (Burgner et al. 1969; Goldman 1960), and deficiencies in other nutrients would limit productivity. The productivity data (Table 2), the diatom abundance (Table 1), and analogy with the Lake Asabatchye findings (Kurenkov 1966), all suggest that favorable growth conditions follow ashfalls. However, if present at all, the stimulatory effect of the Katmai ash clearly is of less magnitude than that of silica enrichment.

Acknowledgments

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Genetic and Environmental Sources of Variation in Length and Weight of Rainbow Trout (*Salmo gairdneri*)

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AULSTAD, D., T. GJEDREM, AND H. SKJERVOLD. 1972. Genetic and environmental sources of variation in length and weight of rainbow trout (*Salmo gairdneri*). J. Fish. Res. Bd. Canada 29: 237–241.

Rainbow trout (*Salmo gairdneri*) of three-year-classes (1967–1969) were produced from random mating, and one-year-class (1970) from inbreeding. The two first-year-classes were fullsib groups. Intraclass-correlations for body length in the 1967-year-class were: 0.16, 0.15, 0.09, and 0.17 at 90, 130, 355, and 485 days of age, respectively. The corresponding estimate for the 68-year-class was 0,25 at age 110 days. Phenotypic correlations between body length at different ages were high within seasons, but low between seasons.

For the 1969-year-class the sire x dam interaction component was negative at ages 150 and 280 days, indicating that nonadditive gene effects were unimportant. Estimated heritabilities ranged from 0.0 to 0.40, those from the sire component being generally higher. Environmental differences between tanks were low, but not ignorable. The 1970-year-class, produced from first generation of fullsib mating, showed significant differences between inbred and control (noninbred) for mortality of eggs and fry, but not for body weight at age 75 days.

AULSTAD, D., T. GJEDREM, AND H. SKJERVOLD. 1972. Genetic and environmental sources of variation in length and weight of rainbow trout (*Salmo gairdneri*). J. Fish. Res. Bd. Canada 29: 237–241.

Les auteurs ont obtenu des truites arc-en-ciel (*Salmo gairdneri*) de trois classes d'âge (1967–69) par croisements au hasard et d'une classe d'âge (1970) par croisements consanguins. Les deux premières classes d'âge proviennent de mêmes parents. Les coefficients de corrélation intraclasse pour la longueur du corps des poissons de la classe de 1967 sont: 0.16, 0.15, 0.09, et 0.17 à l'âge de 90, 130, 355, et 485 jours respectivement. Le chiffre correspondant pour la classe de 1968 est de 0.25 à 110 jours. La corrélation phénotypique entre les longueurs du corps à divers âges est élevée dans les limites intrasaisonnières, mais faible entre les saisons.

Pour la classe de 1969, la composante d'interaction père × mère est négative à l'âge de 150 et 280 jours, ce qui démontre l'insignifiance des effets géniques non additifs. Les estimés d'héritabilité varient de 0.0 à 0.40, les plus hautes valeurs provenant généralement de la composante paternelle. Le milieu ambiant des réservoirs présente de faibles différences qui ne sont toutefois pas négligeables. La classe de 1970, issue de la première génération de croisements pleinement consanguins, affiche des différences significatives entre les sujets consanguins et les témoins (non consanguins) sous le rapport de la mortalité des oeufs et des alevins, mais non du poids du corps à 75 jours.

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THE relative importance of different sources of variation in different characters is little known in fish, particularly concerning the genetic variance. However, for some species investigations have been carried out that give some information about the influence of the genotype.

Donaldson (1968) indicated that in rainbow trout the genotype influenced the observed differences in fecundity, weight, and age at sexual maturity. Unfortunately, there was no control line, and consequently the genetic response to selection could not be estimated. Studies on rainbow trout by Von Limbach (1969) showed great variation in weight gain during the first year. The heritability is expected to be relatively high.

Investigations by Moav et al. (1964) have supplied valuable information about the different sources of variation in the weight of carp. They found the heritability of the family mean at market size to be 0.55 when a sample of 100 fish was measured in 1 lb. The estimate was inflated to 0.75 when the families were tested in four different ponds. These estimates indicated a rather low heritability on individual basis.

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The purpose of this report is to present results obtained from analyses of data from preliminary experiments with rainbow trout (*Salmo gairdneri*).

Materials and Methods

Three-year-classes (1967–69) were produced from random mating, and one-year-class (1970) was used in an inbreeding experiment. The 1967- and 68-year-classes consisted of 22- and 21-fullsib groups, respectively. The mating method to produce the 69-year-class was a factorial within sets. The eggs from each female were divided into two portions. Seven mating sets were formed, each consisting of two males and four females. In the inbreeding experiment there were 52 groups produced from fullsib matings within 9 families, and 19 control groups produced from matings between individuals of the different families.

The 67- and 68-year-classes were reared at Astras' experimental Station at Laxfors, Kungsbacka, Sweden and the 69- and 70-year-classes at the Dal experimental station, Institute of Animal Genetics and Breeding, Agricultural College of Norway.

Results and Discussion

Table 1 shows the mean and standard deviation of body length and weight at different stages. For the 67- and 68-year-classes only the total body length was observed. For the 69-year-class body weight was also measured. Unfortunately, the inbreeding experiment was interrupted 75 days after hatching because of poisoning. Because of the quick decay of dead fry, only body weight could be observed. The actual correlation between body length and body weight is rather high. For the 69-material correlations of 0.98 and 0.94 were found at 150 and 180 days of age, respectively. Therefore, knowledge of one trait gives valuable information about the other.

1967- and 1968-Year-Classes

As these year-classes consisted of only fullsib groups, reliable estimates of the heritabilities cannot be calculated. However, the estimated intraclass correlation for fullsib groups is frequently used as an upper limit for the genetic influence on a trait. In this connection, the value of the intraclass correlation depends on the degree to which there are systematic environmental differences including maternal effects between groups.

The model first assumed for the 67-year-class data was:

$$Y_{ijk} = \mu + a_i + b_{ij} + e_{ijk}$$

where Y_{ijk} = the observation of the k^{th} individual from j^{th} sibgroup and the i^{th} parent location

μ = the theoretical population mean

a_i = effect of the i^{th} parent location (fixed)

b_{ij} = effect of the j^{th} fullsib group within the i^{th} location (random)

e_{ijk} = random error (effect of individuals within groups and locations).

Assumptions — The Y_{ijk} are random variables distributed about a common mean, μ. The components of the model combine additively. $E(b,e) = 0$, $b \sim NID(0,\sigma_b^2)$ and $e \sim NID(0,\sigma_e^2)$. The a_i-term is included in the model because the parents of the 67-year-class came from different locations in Denmark and Sweden. The effect of location was significant only for the first observation. This fact indicates that the effect of location is caused by environmental differences. Therefore, the location classification is included only for the first observation on the 67- year-class. For later observations of both

TABLE 1. Means and standard deviations (SD) of the traits observed.

Year-class	Age in days	No. individuals	Body length (*cm*)		Body wt (*g*)	
			Mean	SD	Mean	SD
1967	90	11168	11.87	2.36		
	130	8197	14.40	2.23		
	355	7407	23.45	2.00		
	483	2831	30.50	2.38		
1968	110	10364	10.69	1.92		
1969	150	2050	9.79	1.14	13.55	4.12
	280	2050	10.13	1.26	13.26	4.37
1970 inbred	75	17581			3.20	1.17
control	75	8842			3.04	1.23

the 67- and 68-year-classes, where all the parents came from one location, a simplified model was used.

Because of unequal subclass numbers the actual k-value had to be estimated.

The estimated variance components and intraclass correlation for the 67- and 68-year-classes are shown in Table 2. The expected composition of the variance component between groups, ignoring epistasy of higher order than two-loci interaction, is $\frac{1}{2}\sigma^2_A + \frac{1}{4}\sigma^2_D + \frac{1}{4}\sigma^2_{AA} + \frac{1}{8}\sigma^2_{AD} + \frac{1}{16}\sigma^2_{DD} + \sigma^2_e$

Here,

σ^2_A = additive genetic variance
σ^2_D = variance due to dominance
σ^2_{AA} = additive x additive gene interaction
σ^2_{DA} = dominance x additive gene interaction
σ^2_{DD} = dominance x dominance gene interaction
σ^2_e = variance due to environmental differences between groups.

If σ^2 and epistasy are ignorable $2 \cdot r$ estimates the relative influence of σ^2_A plus $\frac{1}{2}\sigma^2_D$ on the character. Compared to estimates from halfsib correlation or parent–offspring regression the fullsib correlation tends to yield higher heritability estimates. The reason may partly be the higher environmental correlation within sib groups, and partly an effect of dominance.

The phenotypic correlations between the means of the total body length for the 67-year-class observed at different ages were:

Age in days:	130	355	485
90	0.860	0.593	–0.004
130		0.728	0.205
355			0.573

Rather high phenotypic correlations are obtained within seasons, but rather low between seasons.

TABLE 2. Estimates of variance components and intraclass correlations from the 67- and 68-year-class for total body length.

Age in days		s^2_b	s^2_e	r	s_r
1967	90	0.810	4.407	0.16	0.047
	130	0.779	4.251	0.15	0.042
	355	0.373	3.638	0.09	0.027
	485	0.949	4.745	0.17	0.045
1968	110	0.916	2.811	0.25	0.059

The present data give no possibility for dividing the phenotypic correlation into its components.

The expectation of the covariance between the group means of the same variable, observed at different stages is

$$\frac{1}{n}\left(\mathrm{Cov}(P_{1j},\ P_{2j}) + (n-1)\mathrm{Cov}(P_{1j},\ P_{2k})_{j \neq k}\right)$$

If different numbers are measured at the different stages, n is the greatest number of individuals measured. $\mathrm{Cov}(P_{1j}, P_{2j})$ is the phenotypic covariance between the same individual at the two stages, and $\mathrm{Cov}(P_{1j},\ P_{2k})_{j \neq k}$ is the phenotypic covariance between different individuals of the group at the two stages. If we assume that the phenotype is made up of a genetic and an environmental component, P = G + E, and these components are uncorrelated, the actual covariance will be:

$$\frac{1 + (n-1)}{n} r_g \mathrm{Cov}(G_{1j}, G_{2j}) + \frac{1}{n}\mathrm{Cov}(E_{1j}, E_{2j}) + \frac{n-1}{n}\mathrm{Cov}(E_{1j},\ E_{2k})_{j \neq k}$$

Here, r_g is the genotypic correlation between individuals of the same group. Similar formulae was obtained by Moen (1970).

1969-YEAR-CLASS

The experiment for the 69-year-class was planned with a factorial mating design within sets. Unfortunately, many of the combinations failed to hatch because of specific difficulties after spawning (high water temperature). Out of 56 combinations 29 hatched, and out of these, 16 combinations included two or more replicates. In spite of this serious reduction of the material, the results from the experiment may give some valuable information about the traits concerned.

In the statistical analysis of the data the following model was assumed:

$$Y_{hijkl} = \mu + a_h + s_{hi} + d_{hj} + (sd)_{hij} + k_{hijk} + e_{hijkl}$$

where Y_{hijkl} = the observation of the i^{th} individual in the k^{th} tank with the j^{th} dam and i^{th} sire in the h^{th} set
μ = theoretical population mean
a_h = effect of the h^{th} set
s_{hi} = effect of the i^{th} sire within the h^{th} set

d_{hj} = effect of the j^{th} dam within the h^{th} set

$(sd)_{hij}$ = interaction effects of sire and dam within set

k_{hijk} = effect of the k^{th} tank within the sire-dam combinations

e_{hijkl} = random error (effect of individuals within crosses and tanks).

Assumptions — The Y_{hijkl} are random variables distributed about a common mean, μ. The components of the model combine additively, have zero-covariances, and are normally distributed with the variances σ^2_s, σ^2_d, σ^2_{ed}, σ^2_k and σ^2_e. The expected composition of the variance components from a factorial design, using the general model for the genetic covariance between relatives (Kempthorne 1957) (interaction of a higher order than two-loci interaction is ignored) is:

$$\text{Sire component, } \sigma^2_s = \frac{1}{4}\sigma^2_A + \frac{1}{16}\sigma^2_{AA}$$

$$\text{Dam component, } \sigma^2_d = \frac{1}{4}\sigma^2_A + \frac{1}{16}\sigma^2_{AA} + \sigma^2_M$$

$$\text{Interaction sire } x \text{ dam, } \sigma^2_{sd} = \frac{1}{4}\sigma^2_D + \frac{1}{8}\sigma^2_{AA} + \frac{1}{8}\sigma^2_{AD} + \frac{1}{16}\sigma^2_{DD}$$

where σ^2_M = variance due to maternal effect. The other symbols have been described above.

The data were first analyzed following the "analysis of the unweighted mean" procedure on a within set basis (Becker 1967). Four sets were used, each including two male and two female parents.

The estimated components of variance and heritabilities are shown in Table 3. The standard error of the heritability estimates was calculated as described by Becker (1967).

The sire x dam interaction component was negative at both ages, indicating the nonadditive gene effects to be of little importance. However, the samples were too small to yield any positive conclusions. The lower heritabilities estimated from the dam component indicate the maternal effect to be small.

Assuming the sire x dam interaction to be negligible, the greater part of the data was analysed in a least-squares analysis of variance using the following model:

$$Y_{ijk} = \mu + a_h + s_{hi} + d_{hi} + e_{hij}$$

TABLE 3. Estimated variance components and heritabilities for the 69-year-class.

	Body wt		Body length	
	150 days	280 days	150 days	280 days
s^2_s	0.6378	1.4113	0.0504	0.1542
s^2_d	−0.0603	−0.0932	0.0202	0.0095
s^2_{sd}	−0.1650	−0.2706	−0.0200	−0.0125
s^2_k*	1.0740	0.8092	0.0801	0.0396
s^2_e**	13.9407	15.6490	1.0325	1.2829
h^2_s	0.17	0.32	0.17	0.42
h^2_d	0.00	0.00	0.07	0.03
SE (h^2_s)	0.110	0.216	0.157	0.265
SE (h^2_d)	0.068	0.032	0.101	0.043

*Variance due to differences between tanks within cells.

**Variance within tanks.

The explanation of the components is as before.

This analysis gives five degrees of freedom for sires and nine for dams. Some of the combinations contained only one tank and the effect of tank had to be ignored in the model. The effect of tank is consequently confounded with the sire and dam effects. In calculating the sire and dam components from this analysis the between-tank within-combination mean square was used as the error estimate, thus in a way correcting the estimates for the tank effect.

The following heritabilities were then estimated:

Age:		150 days	280 days
Length	h^2_s	0.16±0.139	0.37±0.225
	h^2_d	0.06±0.086	0.03±0.044
Weight	h^2_s	0.09±0.104	0.29±0.196
	h^2_d	0.06±0.085	0.01±0.050

As should be expected, the estimates are of the same magnitude as those set out in Table 3.

The estimated heritability coefficients are relatively low. However, the coefficients of variation are high, especially for body weight where the estimates ranged from 30 to 40%. Together with the very high fertility this fact indicates that selection for either body weight or length may be successful.

ENVIRONMENTAL DIFFERENCES BETWEEN TANKS

The intraclass correlation for tanks within combinations can be used in evaluating the systematic environmental differences between tanks. The significance of this effect has a great influence on the optimal design of the experiments. Being

ignorable more parent combinations may be included. Probably this effect has to be estimated for several years at each experimental station. The values of the intraclass correlation estimated in this experiment were:

Age:	150 days	280 days
Length	0.064±0.017	0.026±0.010
Weight	0.062±0.017	0.043±0.013

These estimates are low, but not ignorable. The lower estimates for older fish indicate that the tendency of the environmental differences between tanks to accumulate is small.

Inbreeding Experiment

General effects of inbreeding, often found irrespective of species, are higher mortality, lower growth rate and higher frequency of abnormal individuals. Deformations occurring on the fry used in this experiment were reported by Aulstad and Kittelsen (1971).

Total number of individuals and observed mortality of inbred and non-inbred eggs and fry were:

	Eggs		Fry (75 days)	
	Total no.	% dead	Total no.	% dead
Inbred	57477	32.86	27230	28.75
Control	18849	22.24	11810	17.84

The generally high mortality of the eggs was probably caused by rather high-water temperature during hatching (maximum about 13 C).

A chi-square test showed highly significant ($P < 0.001$) differences between inbred and control both for the mortality of the eggs ($\chi^2 = 708.097$) and of the fry ($\chi^2 = 516.810$).

The mean weight of inbred fry was slightly higher than that of the control (Table 1). The data when paired according to dam identification showed no significant difference between the observed weight of inbred and control ($t = 0.926$, $df = 16$). Because one would expect an effect from inbreeding, especially in early growth, this result is surprising. Data from another inbreeding experiment with rainbow trout (von Limbach 1969) indicated that inbreeding growth depression occurs.

The lack of any visible inbreeding growth depression could be caused by higher observed mortality of the inbred compared to the control, provided that mortality preferentially acts on the smallest fry. On the other hand, this result is in agreement with the insignificant estimates of sire x dam interaction in the 1969 material treated previously in this paper.

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Morphometrics of Three Sympatric Arctic Codfishes of the Genera *Arctogadus* and *Gadus*[1]

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Three populations of codfishes inhabit the waters of Cambridge Bay: two belong to the genus *Arctogadus*, the third is *Gadus ogac*. In spite of phenotypic resemblances of some *Arctogadus* specimens to *Gadus*, the two genera are well separated as indicated by significant ($P < 0.05$) differences in otolith shape. Significant differences in 15 out of 27 morphometric characters and in two out of 10 meristic characters, and a different sexual dimorphism indicate that the separation of the Cambridge Bay *Arctogadus* stock in two populations is valid; these populations correspond respectively to the described species *A. borisovi* and *A. glacialis*.

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On trouve trois populations de morues dans le bassin de la baie de Cambridge: deux appartenant au genre *Arctogadus* et une à l'espèce *Gadus ogac*. En dépit de ressemblances phénotypiques entre certains spécimens d'*Arctogadus* et *Gadus*, les deux genres sont nettement distincts comme le suggère une différence significative ($P < 0.05$) dans la forme des otolithes. Des différences significatives dans 15 des 27 caractères morphométriques et deux des 10 caractères méristiques étudiés, de même qu'un dimorphisme sexuel différent justifient la séparation des *Arctogadus* de la baie de Cambridge en deux populations correspondant aux deux espèces décrites, *A. borisovi* et *A. glacialis*.

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THIS work was conducted mainly to verify statistically the presence of taxonomic differences between the two described species of *Arctogadus*, the polar cod *A. glacialis* (Peters) and the east Siberian cod *A. borisovi* Drjagin, and so confirm the results of Nielsen and Jensen (1967) who accepted only two species in their revision of this genus. However, they did not analyse their data statistically and, furthermore, their sample of *A. borisovi* consisted of only 22 preserved specimens of which many were in poor condition. This might have affected their conclusions and did not allow definite rejection of Walters' (1955) hypothesis that the genus might consist of only one species.

The distribution of *Arctogadus* is mainly arctic (Fig. 1). *A. glacialis* occurs more often in deep waters while *A. borisovi* is found in more shallow waters. The two species are generally allopatric except in a few localities of the western Canadian arctic and in the Chukchi Sea; in the latter, one fish out of 35 was *A. borisovi* while the remainder were *A. glacialis* (Nielsen and Jensen 1967). *Gadus ogac* has a more southerly distribution than *Arctogadus* but their range does overlap in a few localities (Fig. 1).

A complete description of the generic characters of *Arctogadus* is given by Svetovidov (1948). Like *Gadus* it belongs to the group of cods with three dorsal fins and two anal fins and is separated from this genus by its lower jaw, which is either equal to the upper jaw or projecting forward, and from *Boreogadus* by the usual presence of palatine teeth and cylindrical and imbricated scales. However, Nielsen and Jensen (1967) found four specimens from the drifting ice station "Charlie" (Walters 1961) lacking palatine teeth but having all other characteristics of *A. glacialis*. The only unambiguous key-character to separate the two species is the presence, in *A. borisovi*, or the absence, in *A. glacialis*, of a mental barbel (Nielsen and Jensen 1967); this character was used in the field to separate the *Arctogadus* specimens.

The specimens used in this work were obtained in Cambridge Bay, N.W.T. Information was collected on *Gadus ogac* because of the resemblance of some *A. borisovi* specimens to this species.

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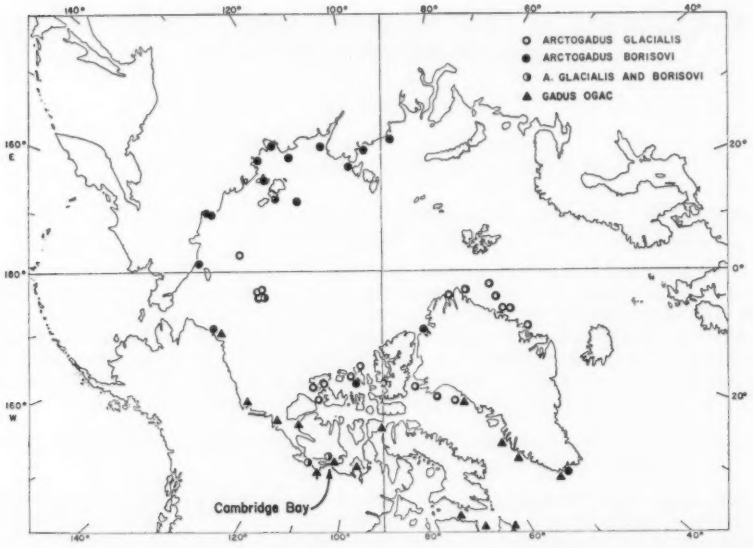

FIG. 1. Distribution of *Arctogadus glacialis* and *A. borisovi* (Nielsen and Jensen 1967) and distribution of *Gadus ogac* (Dunbar and Hildebrand 1952; Hildebrand MS 1948; Pfaff 1937; Walters 1953, 1955). *G. ogac* also occurs south into Hudson Bay and along the Atlantic coast of Canada (Leim and Scott 1966).

Materials and Methods

COLLECTIONS

Specimens and data were collected from the M. V. *Salvelinus* of the Fisheries Research Board of Canada during the summers of 1964–68. Fishing sites were located with a recording echo sounder which revealed fish schools, assumed to be *Arctogadus* spp., close to the bottom of the northeast arm of the basin. Fishing was done using nets with stretched mesh varying between 38 and 140 mm set from surface down to 70 m or less, with hand-lines using baited red and white spoons held at about one meter above the bottom (down to 50m), and on one occasion, with a baited longline set at 50 m.

During the 1964–66 seasons, data recorded from specimens was: total length and weight, gonad weight and maturity, egg diameter, presence or absence of old eggs and their diameter, and weight and a qualitative assessment of stomach contents. Otoliths were taken for age determination and in 1967 and 1968, morphometric measurements and meristic counts were also taken from all specimens of *Arctogadus*.

MEASUREMENTS

All length and weight measurements were taken from fresh specimens. Meristic counts were made from fresh or preserved specimens and otoliths were measured when dried.

Measurements according to the criteria of Hubbs and Lagler (1958) were made on 28 anatomical structures. Table 1 lists 27 of these characters. Measurements of length of the lower jaw were rejected on account of discrepancy between years as explained later. The structures and distances measured are indicated in Fig. 2. Measurements <150 mm were made with dial calipers to ± 0.5 mm precision. Those >150 mm were obtained with a ruler with a precision of ±2 mm on lengths up to 600 mm. Fork lengths and total lengths were measured with a standard fish-measuring board.

Counts on meristic characters, with the exception of vertebrae, were made in the field. Vertebrae, excluding the urostyle, were counted in the laboratory and their number confirmed by making two additional counts. Gill rakers were counted at least twice. Other meristic character counts were checked and revealed no error on counts less than 15 but an error of ±1 on counts greater than 15.

Otoliths were evaluated as systematic characters and maximum length, width and thickness, including curvature if present, of right and left saccular otoliths was measured to ±0.1 mm with dial calipers.

ANALYSIS OF DATA

Regressions of morphometric measurements with standard length and otolith width with thickness measurements were calculated according to Mather (1964). Regression coefficients for both groups of data were highly significant ($P < 0.001$). Meristic characters were studied by variance analysis (Mather 1964). Morphometric measurements were regressed against standard length of the fish and were tested for difference between

TABLE 1. Specific differences between the two *Arctogadus* spp. from Cambridge Bay. Morphometric characters in italics differ significantly between species. The probability of no difference in slope (S) and position (I) between the specific regression lines are given. Extreme values and mean (in parentheses) expressed as percent of standard length, are given. The fourth figure is the number of specimens.

Character	*A. glacialis*				*A. borisovi*				Probability S	Probability I
Standard length, *mm*	169	(325)	462	63	180	(350)	477	61	–	–
Head length	25.1	(28.1)	30.7	63	25.8	(28.9)	33.2	61	>.05	<.01
Snout length	7.4	(8.3)	9.4	63	8.0	(9.1)	11.2	61	=.01	<.01
Post-orbital	9.3	(12.0)	14.5	63	10.3	(12.6)	14.7	61	>.05	<.01
Diam orbit	6.1	(7.2)	8.7	63	5.5	(6.7)	8.2	61	<.01	<.01
Diam dye	4.2	(5.9)	7.2	63	4.6	(5.5)	7.2	61	>.05	<.01
Fleshy interorbital	5.2	(6.0)	7.0	62	5.7	(6.6)	7.8	61	>.05	<.01
Bony interorbital	2.7	(3.6)	4.7	62	3.1	(4.4)	5.5	61	<.01	<.01
Upper jaw	10.9	(12.3)	13.4	63	11.0	(12.7)	14.9	61	>.05	<.01
Preanal 1 length	49.1	(53.0)	60.3	63	49.4	(54.9)	60.2	61	>.05	>.05
Preanal 2 length	70.5	(75.3)	79.6	63	72.5	(75.3)	79.1	61	>.05	>.05
Predorsal 1	31.1	(34.4)	38.4	63	31.9	(34.8)	38.1	34	>.05	>.05
Predorsal 2	47.4	(51.3)	55.3	63	48.2	(51.6)	54.8	61	>.05	>.05
Predorsal 3	68.5	(73.2)	76.5	63	69.9	(73.2)	76.8	61	>.05	>.05
Prepectoral	28.0	(30.5)	33.2	63	29.2	(31.5)	34.5	61	>.05	<.01
Preventral	24.9	(28.3)	33.7	63	24.8	(29.5)	35.9	61	>.05	<.01
Base dorsal 1	8.8	(11.2)	14.5	63	9.0	(11.3)	14.3	61	>.05	>.05
Base dorsal 2	15.9	(18.8)	21.7	63	16.0	(19.2)	21.8	61	>.05	>.05
Base dorsal 3	13.0	(15.3)	18.5	63	12.7	(15.2)	17.1	61	>.05	>.05
Base anal 1	16.9	(19.3)	23.7	62	15.4	(18.9)	23.9	60	>.05	>.05
Base anal 2	12.4	(14.9)	17.2	62	13.2	(15.1)	17.8	61	>.05	>.05
Ventral fin	13.6	(19.9)	28.5	62	14.1	(18.2)	23.4	34	>.05	=.02
Pectoral fin	16.3	(18.3)	22.2	62	16.7	(18.5)	21.6	34	>.05	>.05
Barbel length	0.0	(0.5)	1.4	30	2.3	(3.6)	4.8	61	<.01	<.01
Caudel depth	3.1	(3.6)	4.7	63	3.3	(3.9)	4.7	34	>.05	<.01
Caudal peduncle length	10.2	(11.6)	14.7	62	10.1	(11.7)	13.2	34	>.05	>.05
Total length	108.0	(110.9)	112.9	62	109.0	(111.5)	114.1	61	>.05	<.01
Fork length	106.6	(108.3)	109.9	62	106.2	(108.8)	110.9	61	>.05	<.01

the 2 years of sampling. When significant differences between years were noted, the character was not studied any further, as this suggested discrepancy in the measuring method between the two summers. All groups of data were tested for differences between sex and species; when significant differences between sex were observed, equal numbers of males or females were pooled to give differences between species.

Results and Discussion

COMPARISON OF ARCTOGADUS AND GADUS

Three types of gadids were captured coincidently in the basin of Cambridge Bay and were identified tentatively as *Arctogadus glacialis*, *A. borisovi*, and *Gadus ogac*. Since *A. borisovi* appeared superficially intermediate between *A. glacialis* and *G. ogac*, it was important, therefore, to show that the fish identified as *A. borisovi* were not in fact *G. ogac*. To test this possibility, 48 *A. borisovi*, 81 *A. glacialis*, and 31 *G. ogac* were examined and grouped according to the following categories:

(1) Typical *Gadus ogac* form; (2) Similar to *G. ogac* with brown mottled colour; lower jaw only as long as upper; scale pattern that of *Arctogadus*; (3) Similar to *G. ogac* with brown mottled colour; lower jaw slightly longer than upper; (4) Similar to *Arctogadus* with lower jaw longer than upper; body colour generally brown; (5) Similar to "typical" *Arctogadus* with body colour more black than brown or entirely black.

Specimens of *G. ogac* were examined mainly to establish any resemblance with *Arctogadus*. The results of this examination are illustrated in Fig. 3. While specimens of *A. glacialis* remain very close to the "typical" *Arctogadus* (category No. 5), those of the *A. borisovi* type have evolved some resemblance with *G. ogac* (category No. 1) with more than 64% being of types 2, 3, and 4 as opposed to 21% for the same categories in *A. glacialis*. *Gadus ogac* remains

typical, the 31 specimens examined showing no resemblance to *Arctogadus*.

These observations demonstrate the phenotypic stability of both *A. glacialis* and *G. ogac* and the phenotypic variability of *A. borisovi* between the two other species of fish. Two questions were put forward following these observations. First, could this variation be the result of a breakdown of the genetic isolating mechanisms between *G. ogac* and *A. glacialis* following compression of the two species into a restricted environment, though giving rise to a variable hybrid fitting the description of *A. borisovi*? A positive answer was not expected as intergeneric hybrids in fish have not been commonly reported in

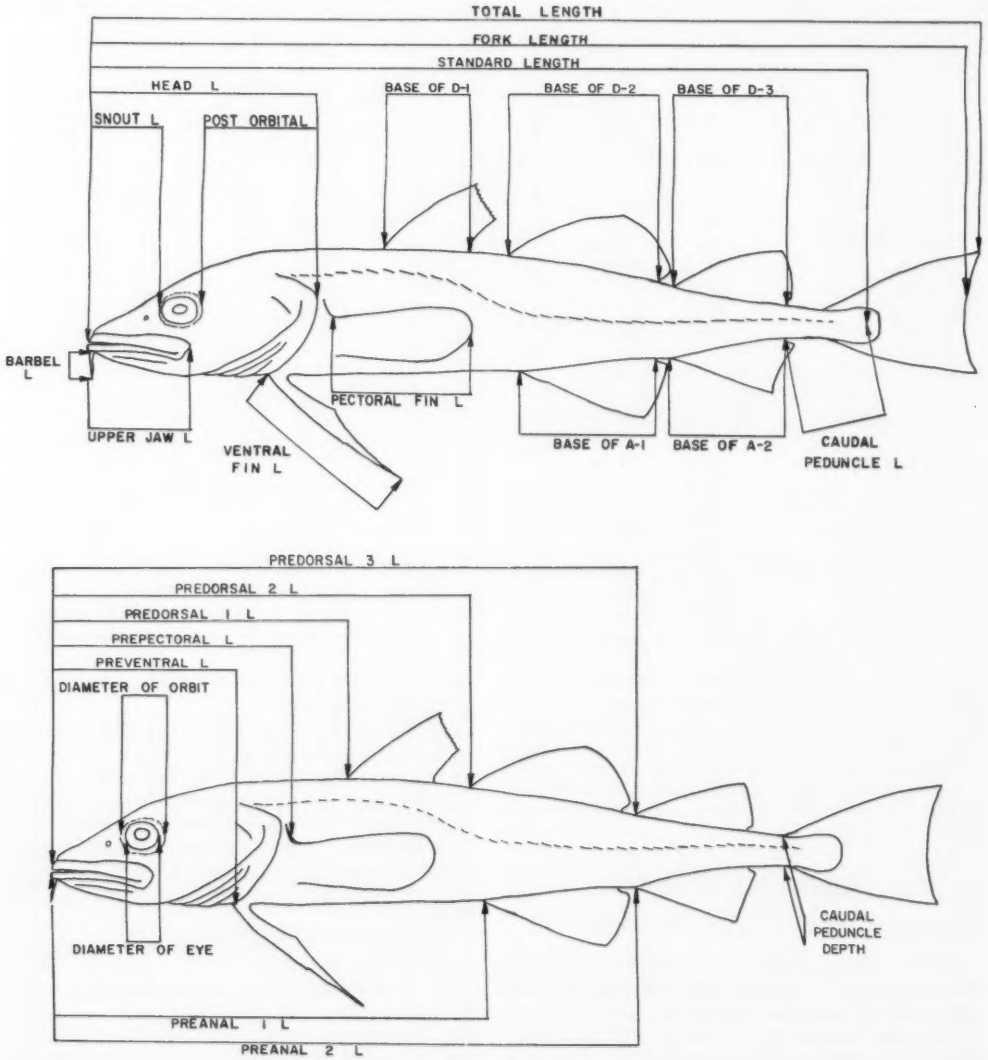

FIG. 2. Morphometric measurements of *Arctogadus glacialis* and *A. borisovi*. Each measurement was the distance between two arrows for a given morphometric character. L is length; D is dorsal fin; A is anal fin. Not illustrated are widths of fleshy and bony interorbitals.

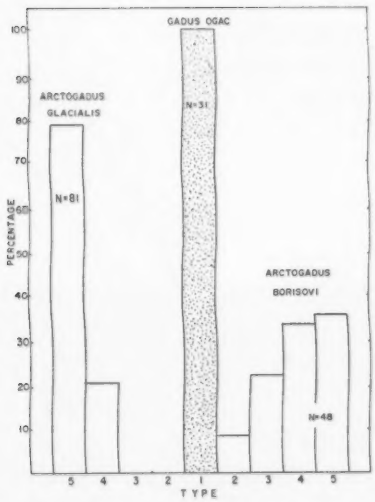

FIG. 3. Percentage distributions of phenotypic variations of *Gadus ogac* (center), *A. glacialis* (left), and *A. borisovi* (right). Type 1 is typical *G. ogac*; Type 5 is typical *Arctogadus*; Types 2, 3, and 4 are intermediate between 1 and 5.

the literature. A second possibility was that resemblance might be explained by assuming that the two species occupy similar ecological niches when allopatric. This is indicated by habitat and food preferences described by Svetovidov (1948) and Moskalenko (1960) for *A. borisovi*, and by Leim and Scott (1966) for *G. ogac*. This niche similarity could result in convergent evolution and give rise to two very similar species in two different genera.

This second hypothesis was supported by consistent differences between otoliths of the two genera. Otoliths might be expected to be intermediate in hybrids, but are unlikely to respond, like body colour, to similarities of habitat and food, under selective pressure.

The difference in form of otoliths is shown in Fig. 4. *Arctogadus* otoliths are flat while those from *Gadus ogac* are curved. Ratios of otolith width on otolith thickness for each of *G. ogac*, *A. borisovi*, and *A. glacialis* indicated little resemblance between *Arctogadus* and *Gadus* otoliths in spite of the superficial phenotypic resemblances of the two genera (Fig. 5).

Regression of otolith width on otolith thickness indicated that the fitted lines of both *A. borisovi* and *A. glacialis* differed significantly ($P < 0.001$) in slope and position, from the fitted line of *G. ogac* (Fig. 6). The fish tentatively assigned to the two *Arctogadus* species did not differ significantly with respect to these characters. These results thus confirmed the field separation of most of the fish captured into either the *Gadus* or the *Arctogadus* group.

MORPHOMETRY

The examination of 27 comparable characters by means of regression analysis indicated the following significant differences between *A. borisovi* and *A. glacialis*: specific differences were noted in 15 of the 27 morphometric characters studied (Table 1); sexual dimorphism was observed in *A. borisovi* in four morphometric characters and in *A. glacialis* in eight characters, only one of which, the length of the ventral fin, was common to the two species (Table 2). Previously, sexual dimorphism in *Arctogadus* spp. had been shown only for the ventral fin (Johansen 1912; Jensen 1948). Comparison with published data (Andriyashev 1957; Nielsen and Jensen 1967; Svetovidov 1948) generally indicates good agreement; differences in some characters are probably due to slight variations in measuring techniques.

MERISTIC CHARACTERS

Eight of 10 meristic characters were examined by analysis of variance; the other two exhibited no variability between sex or species. The available data were randomly sampled giving a total of 17 individuals for each of the four classes (two species and two sexes). The frequency distribution of counts are illustrated on Fig. 7.

Two meristic characters differed significantly ($P \leq 0.02$) between species. *Arctogadus borisovi* had a smaller mean number of rays (11.5) than *A. glacialis* (11.7) in its first dorsal fin, while *A. glacialis* had a smaller mean number of rays (20.8) than *A. borisovi* (21.6) in its second anal fin. There was also significant sexual dimorphism ($P = 0.02$) in one character, males of both species having on the average more rays in the first dorsal fin.

Mean number of gill rakers did not differ significantly between species or sexes. This result differed from that of Nielsen and Jensen (1967) who used this character in their key to the two species of *Arctogadus*. They observed less rakers in *A. glacialis* than in *A. borisovi* (mean of 30 against 33) but confidence in their *A. borisovi* sample, being based on only 12 specimens, is low.

Mean number of vertebrae (Fig. 7) was similar for both species (58.10 for *A. borisovi*, 58.04 for *A. glacialis*) but the range was greater in *A. borisovi* (56–60) than in *A. glacialis* (57–59). The apparent bimodal distribution of *A. borisovi* can be assumed to be a consequence of the small sample size. Nielsen and Jensen (1967) obtained a high variation in the num-

bers of vertebrae for both species. However, their sample originated from widely separated arctic locations, a fact which could account for this variation.

General Discussion

The significant differences between morphometric and meristic characters of these two closely associated populations of *Arctogadus* spp. found in the basin of Cambridge Bay indicate that the populations are reproductively isolated and therefore valid species. On the basis of these characters, the two populations correspond to *A. borisovi* and *A. glacialis* as described by Nielsen and Jensen (1967).

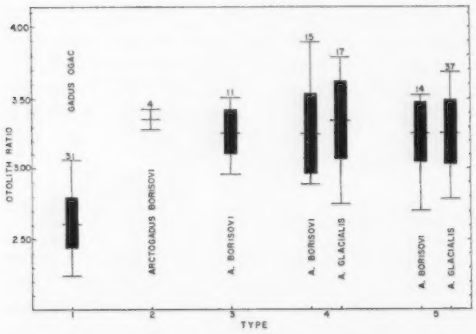

FIG. 5. Otolith ratios (width/thickness) for *Gadus ogac*, *Arctogadus borisovi*, and *A. glacialis*. Type 1 is typical *G. ogac*; type 5 is typical *Arctogadus*; types 2–4 are intermediate between 1 and 5. Black rectangles indicate one standard deviation; mean, range, and number of specimens examined are also included.

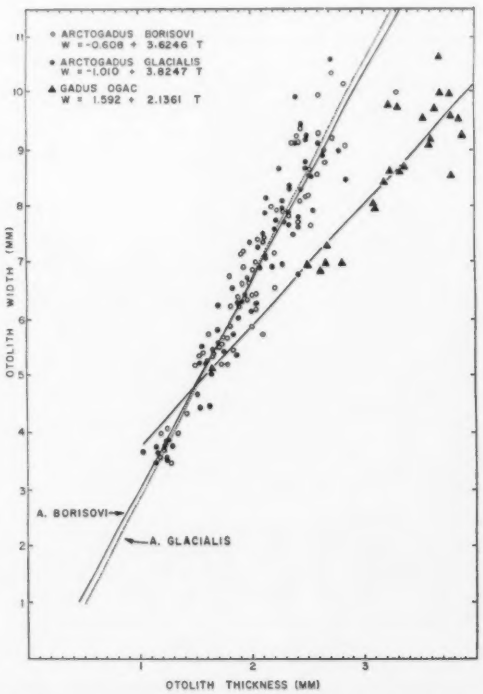

FIG. 6. Regression of otolith width on otolith thickness for *Gadus ogac*, *Arctogadus borisovi* and *A. glacialis* from Cambridge Bay. The fitted line for *G. ogac* differs significantly ($P < 0.001$) from those for *A. borisovi* and *A. glacialis*. Fitted lines for the two *Arctogadus* do not differ significantly ($P > 0.05$) one from the other.

TABLE 2. Morphometric characters showing significant differences between sexes of *Arctogadus glacialis* (G) and *A. borisovi* (B) from Cambridge Bay. The probabilities of no difference between slopes and positions of regression lines of each sex, are given with extreme values (– and +) and mean ($\overline{\%}$) expressed as per cent of standard length. n = number of specimens in sample.

		Male				Female				Probability	
Character	Species	–	$\overline{\%}$	+	n	–	$\overline{\%}$	+	n	Slope	Position
Fleshy interorbital	G	5.2	(6.1)	6.9	31	5.3	(5.9)	7.0	32	0.05–0.02	0.02–0.01
Bony interorbital	G	2.8	(3.6)	4.7	31	2.7	(3.5)	4.3	32	>0.05	0.05–0.02
Predorsal 1 length	B	31.9	(34.3)	37.5	17	32.4	(35.5)	39.4	44	>0.05	0.02–0.01
Base anal 1 length	G	17.8	(20.0)	23.7	31	16.9	(18.7)	21.6	32	>0.05	<0.001
Base anal 2 length	G	14.0	(15.5)	17.2	31	12.4	(14.4)	16.4	32	0.02–0.01	<0.001
Ventral fin length	G	18.2	(23.0)	28.5	31	13.6	(16.7)	20.4	32	<0.001	<0.001
Ventral fin length	B	17.8	(20.2)	23.4	17	14.1	(16.3)	19.1	44	>0.05	<0.001
Pectoral fin length	G	17.1	(18.9)	22.2	31	16.3	(17.7)	19.8	32	>0.05	<0.001
Caudal depth	B	3.3	(3.8)	4.7	17	3.4	(4.0)	4.4	44	>0.05	<0.01
Total length	G	109.4	(111.2)	112.9	31	108.0	(110.7)	112.4	32	>0.05	<0.01
Fork length	G	107.4	(108.5)	109.9	31	106.6	(108.1)	109.1	32	>0.05	<0.01
Caudal peduncle length	B	10.4	(11.7)	12.8	17	9.5	(11.0)	13.0	44	>0.05	<0.01

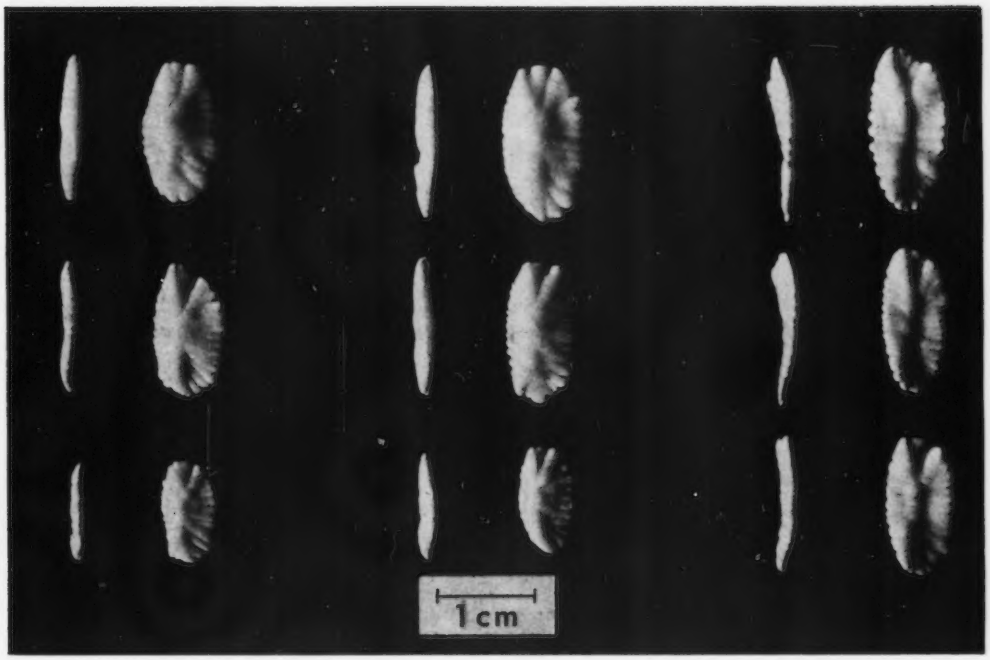

FIG. 4. Otolith forms of the three codfishes examined. The following values are total lengths of fish. Left: *Arctogadus borisovi*, 466, 406, and 315 mm; center: *A. glacialis*, 462, 406, and 315 mm; right: *Gadus ogac*, 467, 407, and 398 mm. *Arctogadus* spp. otoliths are flat while *G. ogac* otoliths are curved when seen on edge.

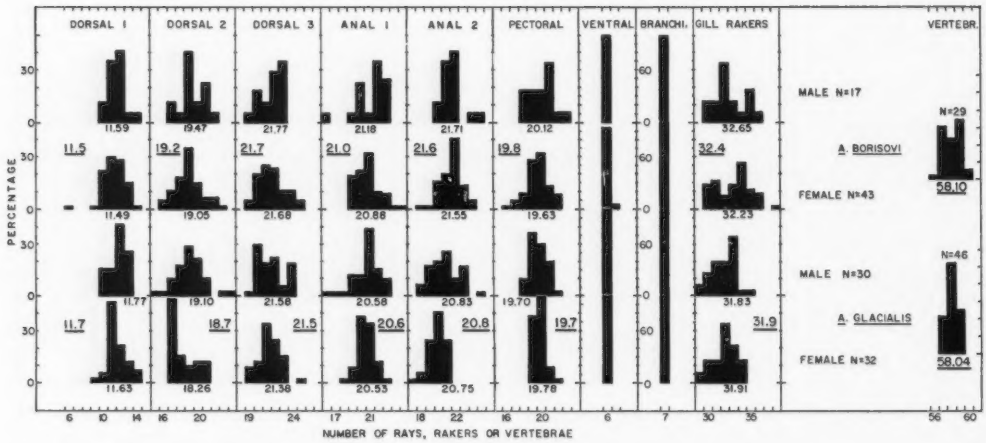

FIG. 7. Percentage distributions of counts of the rays of seven fins, branchiostegal rays, gill rakers, and vertebrae. Distributions are given for males and females, for the first nine meristic characters. Distributions of counts of vertebrae are given for species only because of small sample size. N is number of specimens examined. The mean of each distribution is given under the frequency histograms; underlined figures are means of combined male and female data (weighted in *A. borisovi* to correct for the large difference of sample size of each sex).

The hypothesis that *A. borisovi* and *A. glacialis* are two types of a polymorphic species should be examined. If this were the case, the two types would be found together where *Arctogadus* occurs. However, the two types are generally allopatric, which does not support this theory. Furthermore, a simple two-allele polymorphism would be unlikely to affect the large number of characters in which the two types differ. These observations and the results therefore tend to refute the opinion that this genus might consist of only one species as proposed by Walters (1955), and support the conclusions of Andriyashev (1957) and Nielsen and Jensen (1967) that there are two valid species.

The reason for the absence of *Arctogadus* from the southern Canadian arctic archipelago, except in Cambridge Bay and possibly Port Epworth, is not clear. The mainland coast of the western Canadian arctic has been extensively surveyed by the Fisheries Research Board of Canada from the Alaska border eastward to Cambridge Bay; the latter is the only locality where the genus was found (I. G. Gidney personal communication). The bay is a deep basin (80 m) with a shallow entrance (12 m); no *Arctogadus* were caught in the entrance or outside the bay. This genus was also reported from Port Epworth, some 200 miles (320 km) to the southwest of Cambridge Bay (Walters 1953) but a search there in late August 1970 failed to find any *Arctogadus* spp. or *Gadus* spp. (I. G. Gidney personal communication).

Possibly conditions became unfavourable to *Arctogadus* through shallower water resulting from the postglacial land rise, which "landlocked" the small population in Cambridge Bay, through warmer postglacial temperatures (Zenkevitch 1963), or competition from other gadid species that invaded the southern part of the archipelago (Walters 1955).

Acknowledgments

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Effects of Acclimation and Acute Temperature Experience on the Swimming Speed of Juvenile Coho Salmon[1]

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Swimming performance of juvenile coho salmon (*Oncorhynchus kisutch*), 7.5–9.5 cm in total length, was investigated in a stamina tunnel, generally at 3 C intervals of temperature over the range of thermal tolerance.

Optimum (ultimate maximum) performance (5.8 lengths/sec) occurred at a combination of acclimation and test temperatures near 20 C. A declining ridge of sub-optimum performance (*test temperature ridge*) was found at acclimation temperatures below 20 C; maximum performance at each acclimation temperature level was found on the ridge at test temperatures higher than those of acclimation. Conversely, maximum performance at given test temperatures occurred on a second ridge (*acclimation temperature ridge*) at acclimation temperatures near those of testing. There was an apparent shift in location of the acclimation temperature ridge, indicative of seasonal performance compensation and improved capacity to perform at low acclimation temperatures during the winter period. At test temperatures below 5 C, maximum performance occurred at acclimation temperatures of about 6–8 C. Lowest performance within the zone of thermal tolerance was associated with acclimation and test temperatures of 2 C.

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Les auteurs étudient la performance natatoire de jeunes saumons coho (*Oncorhynchus kisutch*) de longueur totale de 7.5 à 9.5 cm dans un tunnel de résistance. En général, les essais ont été faits à des intervalles de température de 3 C sur toute la gamme de thermotolérance de l'espèce.

La performance optimale (maximum final) de 5.8 longueurs/s se situe à des températures d'acclimatation et d'essai se rejoignant aux environs de 20 C. A des températures d'acclimatation inférieures à 20 C, une arête déclinante de performance sous-optimale (*arête de température d'essai*) est évidente; à des températures d'essai plus élevées que celles d'acclimatation, il se produit sur l'arête un maximum de performance à chaque palier de température d'acclimatation. Inversement, à des températures d'acclimatation voisines de celles d'essai, il se produit sur une seconde arête (*arête de température d'acclimatation*) un maximum de performance à des températures d'essai données. L'emplacement de l'arête de température d'acclimatation semble se déplacer, signe d'une performance compensatrice saisonnière et d'une plus grande capacité de performance aux basses températures d'acclimatation en hiver. A des températures d'essai inférieures à 5 C, la performance maximale a lieu à des températures d'acclimatation voisines de 6–8 C. La plus faible performance dans la zone de thermotolérance est associée à des températures d'acclimatation et d'essai de 2 C.

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TEMPERATURE experience the organism can tolerate indefinitely is quantitatively defined as the zone of thermal tolerance (Fry 1947), and has been measured for coho salmon (*Oncorhynchus kisutch*) by Brett (1952). Within the zone of tolerance, the existence is postulated of other more restrictive fields of response to temperature (Brett 1958). These fields relate the effects of temperature to levels of specific functions, and most often have been measured in terms of locomotor ability, metabolism, growth, food conversion efficiency, reproductive capacity, embryonic development, and aggregation of fishes (Brett 1970; Alderdice 1972). One such field, temperature effects on locomotor performance of young coho salmon, is examined here. Performance is examined at temperatures of acclimation, as well as at those (acute) temperatures to which the animal has not had the opportunity to acclimate.

Swimming performance of young coho salmon is associated with an ability to maintain position in flowing water, obtain food, escape predators, or defend territory. Swimming capacity is also related to the energy available to the fish after maintenance requirements for metabolism have been met (Brett 1965), and thus is related to scope for activity (Fry 1947). Swimming performance is also size-dependent, and varies approximately according to the square root of body length (Bainbridge 1960; Brett 1965; Fry and Cox 1970).

Methods employed herein for determination of swimming speeds are essentially those described by Brett (1967). Performance has been measured in terms of *critical swimming speeds* by applying increments of increased velocity until fatigue occurs in the test subjects. The method provides good approximations to *maximum sustained swimming speeds* derived by fixed velocity testing techniques.

Materials and Methods

SOURCE AND CULTURE OF FISH

A stock of 2500 underyearling coho salmon collected in September 1968 from Kincade Creek, a tributary of the Little Qualicum River, Vancouver Island, B.C., was held in an outdoor tank at the Nanaimo laboratory during the experimental period (September 1968–May 1969). A continuous inflow of fresh water provided a moderate level of continuous swimming activity. The fish were subject to natural photoperiod, and seasonal and daily water temperature fluctuations. Pelleted food was given daily, supplemented for the first few months with frozen brine shrimp (*Artemia*).

ACCLIMATION

Groups of approximately 100 fish were moved indoors as required into 80-liter acclimation tanks. Fish to be acclimated were selected for a given total length (±0.25 cm) to standardize the size of experimental fish for each test series.[1] Mean length of experimental groups was manipulated to some extent by selection for initial size, in anticipation of growth expected and final size required at the end of the acclimation period.

Test fish were held in the acclimation tanks at the required temperature (±0.1 C) for at least 2–3 weeks before use, the period being dependent on the direction and magnitude of the temperature change required (Brett 1952). Actual acclimation periods (Griffiths MS 1969) were usually longer than the minimum suggested. A small flow of water (400 ml/min) was added to each acclimation tank to provide water exchange. Pumps recirculated the water in each tank, producing a current averaging 6–8 cm/sec.

Fluorescent "daylight" lamps provided illumination. Photoperiod was regulated to provide normal day length ±30 min. Fish were fed daily on the same diet as the outdoor stock. Food was withheld from test fish for a minimum of 12 hours prior to their use in the stamina tunnel.

SWIMMING SPEED APPARATUS

A recirculating water tunnel was used to measure swimming speeds (Fig. 1). Water was circulated by a five-bladed propeller, belt-driven by a $\frac{3}{8}$ hp constant speed electric motor through an interposed hydraulic variable-speed drive. Major components of the tunnel were constructed of glass fibre reinforced plastic. Total volume of the tunnel in operation was about 450 liters. Temperatures were maintained to ±0.1 C of required levels.

Stainless steel turbulence screens produced microturbulent flow at the upstream end of the experimental chamber, which was clear acrylic tubing $5\frac{3}{8}$ inches I.D. × 24 inches long, and provided an extremely flat velocity profile in this test section. Alternating black and white plastic strips on the top and bottom outer surfaces of the experimental chamber provided visual cues for orientation of swimming fish. At the downstream end was an electric barrier (three charged graphite rings) which was strongly illuminated to further induce test fish to remain upstream from it. As a fish fatigued it was forced through the electric field onto the nylon screen at the entrance to the recovery section. The screen was then raised to recover the fatigued fish.

Preliminary tests established the relation between water velocity in the experimental section and propeller shaft rotation. The turbulence screens tended to accumulate debris, causing drift in the relation between water velocity and shaft rotation. After the problem was recognized, the screens were cleaned after each test and the velocity calibration checked weekly.

Acclimation and test temperatures were seldom identical. It was desirable to maintain test fish at the temperature of acclimation until they had entered the experimental chamber, and provide them with an op-

[1]Total length (hereafter called length) is the distance between the snout and a line joining the tips of the caudal fin in its normal position.

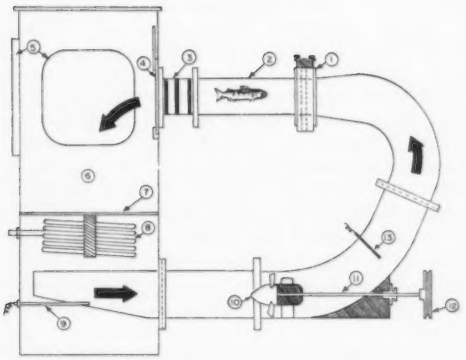

FIG. 1. Diagrammatic view of water tunnel. Arrows indicate direction of water flow. 1, turbulence screens; 2, experimental chamber; 3, electric barrier section; 4, removable rear screen; 5, observation ports; 6, chamber for recovery of fatigued fish; 7, screen; 8, cooling coils; 9, quartz heaters; 10, propellor; 11, propellor shaft; 12, drive pulley; 13, temperature sensor.

portunity to recover from the effects of transfer from the acclimation tanks. An entry device was constructed from a large plastic funnel positioned at the top of the recovery section. For a typical test, 10 coho salmon were placed in the entry device through which water was circulated from the appropriate acclimation tank. The fish were transferred to the device in semi-darkness, and held in darkness for a period of 1 hr. A stopper was then removed from the entry device, allowing the fish to swim into the experimental chamber through a connecting tube. The entry device and connecting tube were then removed, the nylon screen replaced at the rear of the test section, and the electric barrier switched on. All tests were conducted in a darkroom with a one-way mirror positioned between the illuminated experimental section and the operator.

PRESENTATION OF DATA

In each test, water velocity was increased incrementally until the last fish in the sample fatigued. Velocity increments of approximately one-eighth the maximum swimming speed (estimated from preliminary tests) were applied for 1-hr periods, resulting in fatigue of test fish after 7–10 hr of swimming. Velocities associated with fatigue of individual fish in a sample were estimated by interpolation in cases where fatigue did not occur exactly at the beginning or end of an hourly period (Brett 1964).

Median performance of groups of 10 fish used in each experiment was determined graphically by plotting logarithms of critical swimming speed (cm/sec) against cumulative percent of fish fatigued (probit scale). The transformation linearized most of the data. However, about 12% of the test distributions of fatigue velocities showed evidence of mixed fatigue effects or compound responses to velocity (Finney 1952, p. 122 et seq.). "Split probit" lines were fitted by eye, and median performance was estimated from the split plots.

Initially it was assumed that size variations within test samples of fish might affect the order of fatigue. Hence, critical velocity might be better calculated using logarithms of swimming speed in body lengths/sec (L/sec), instead of in cm/sec, for individual fish. Tests indicated that either method was satisfactory. Although variations in size of fish within samples appeared to pose no problem, the possibility remained that variations in size between samples might bias measures of temperature-dependent performance. Accordingly, individual fatigue velocities within samples were derived in cm/sec, and the median critical swimming speed of each sample was recorded in L/sec by division by the mean length of the sample.[2]

Performance within the zone of tolerance was examined at 3 C intervals of acclimation and test temperature from 2–23 C. In some cases test temperatures > 23 C were employed. These and several other acclimation–test temperature combinations outside the zone of tolerance were selected on the basis of expected resistance times (Brett 1952) to first mortalities being considerably greater than the period required to complete a performance test. Even so, in a number of these cases post-fatigue mortality occurred when test groups were returned to appropriate acclimation temperatures for post-experimental observation (Griffiths MS 1969).

Two complete series of tests were performed in the temperature space. For each series a response surface was constructed to show the effects of acclimation and acute temperature experience on critical swimming speed. Methods of response surface analysis were employed (Box 1956; Box and Tidwell 1962; Lindsey et al. 1970; Lindsey and Sandnes MS 1970). Hence

$$Y^{\gamma} = b_0 x_0 + b_1 x_1^{\alpha_1} + b_2 x_2^{\alpha_2} + b_{11} x_1^{2\alpha_1} + b_{22} x_2^{2\alpha_2} + b_{12} x_1^{\alpha_1} x_2^{\alpha_2}$$

where
- Y = critical swimming speed (L/sec)
- x_1 = acclimation temperature (C)
- x_2 = test temperature (C)
- $\alpha_1, \alpha_2, \gamma$ = power parameters, estimated by maximum likelihood procedure (Lindsey et al. 1970)

Given the data and the model, the surfaces so constructed represent minimum variance estimates of the relation between swimming speed and acclimation and test temperature.

During these experiments it was necessary to conduct tests both day and night. A series of eight tests was completed at one set of acclimation- and test-temperature conditions, four between 0800 and 2000 hr, and four

[2]Tables of original data may be obtained on request from the Biological Station, Nanaimo.

between 2000 and 0800 hr. The resulting critical speeds (L/sec) were:

	Night	Day
	5.14	4.14
	4.62	5.06
	5.11	5.42
	5.24	5.07
Mean	5.03	4.92
Variance	0.2307	0.9005

Hence $s^2 = (0.2307 + 0.9005)/6 = 0.18853$,

$s_{\bar{x}} = (2(0.18853)/4) = 0.307$,

$t = 0.11/0.307 = 0.390\ (P < .50)$,

and the differences between the means of the day and night tests are not considered significant. Pooling the results, the mean of the eight tests (±1 standard deviation) is 4.98 ± 0.40 L/sec, indicative of the variability in swimming speed estimates which might be expected over the field of temperature levels examined.

Results

First Series

This series of performance tests over the temperature space was completed between September 19, 1968, and February 6, 1969. Initially, critical swimming speeds were estimated at six levels of equal acclimation and test temperature. For these tests, cruising speeds determined for coho by Brett et al. (1958) were used as prior performance estimates. From these initial tests, the velocity increments to be applied to the various performance experiments at each acclimation temperature were progressively estimated.

During subsequent tests in the first series, a progressive change in performance became evident relative to the initial tests. The cause was discovered to be accumulation of debris on the turbulence screens. A calibration error was determined, and the affected data (acclimation temperatures of 2–17 C) were adjusted accordingly.

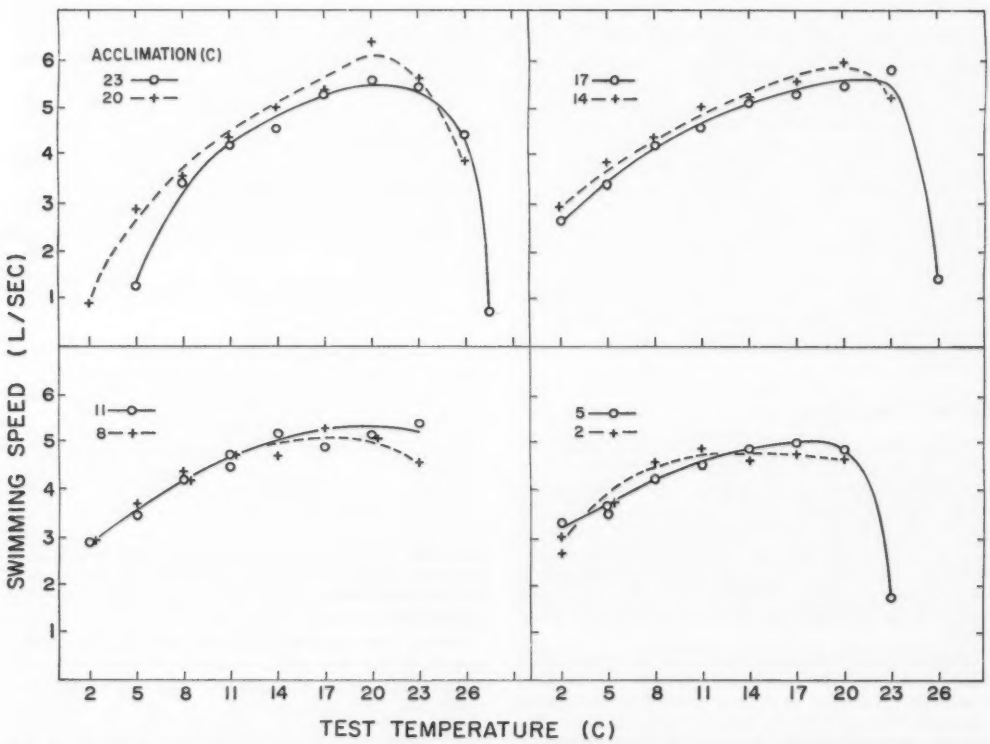

FIG. 2. Critical swimming speeds of young coho salmon (L/sec) determined acutely for temperatures between 2 and 26 C. Curves are eye-fitted. First series.

At each of the eight acclimation temperatures, acutely determined critical swimming speeds increased gradually with higher test temperatures to a maximum near a test temperature of 20 C (Fig. 2). In ad dition, the highest performance level obtained was for the maximum of the 20 C acclimation series. At test temperatures higher than 20 C there was, in general, a marked reduction in performance.

The estimates of critical swimming speed were subjected to response surface analysis using the nonlinear polynomial as a model. Hence

$$Y^{2.37} = 15.527 + 0.647x_1^{1.16} + 0.063x_2^{2.35} - 0.029x_1^{2.32} - 4.47 \times 10^{-5}x_2^{4.70} + 1.22 \times 10^{-3}x_1^{1.16}x_2^{2.35}$$

where $\alpha_1, \alpha_2, \gamma = 1.161, 2.352, 2.371$.

The relative likelihood (Lindsey et al. 1970) of a linear model (with $\alpha_1 = \alpha_2 = \gamma = 1$) providing an adequate fit to the data, as compared with the nonlinear model employed, is 1.7×10^{-18}, or nearly zero.

Variance is partitioned into components associated with regression on linear, puadratic, and interaction terms (Table 1). The analysis indicates that the linear test temperature component could be eliminated without greatly affecting the adepuacy of the model (see footnote 3, Table 1). However, for the ensuing analysis all terms are retained as the best estimates available.

The response surface (Fig. 3) is constructed relating critical swimming speed (L/sec) to levels of acclimation and test temperature. The canonical equation of the surface is:

$$Y' - 65.532 = -0.0293Z_1^2 - 3.1908 \times 10^{-5}Z_2^2$$

where Y' = critical swimming speed in terms of Y^{γ}
$65.532 = Y_s^{\gamma}$, swimming speed at the centre of the surface, S
Z_1, Z_2 = canonical variables, linear combinations of the x^{α} variables

Both terms on the right-hand side of the canonical equation are negative; hence the surface is a modified ellipse with a maximum at the centre. Transposed to original units, the response at the centre of the surface is 5.84 L/sec, calculated to occur at:

S = (acclimation temperature 22.03 C; test temperature 20.45 C)

In Fig. 3, the axes of two ridge systems are indicated at *a*: those test temperatures for which performance is maximal at given acclimation temperatures, and *b*: those acclimation temperatures for which performance is maximal at given test temperatures.

TABLE 1. Analysis of variance of the data for the first series of performance tests according to the nonlinear model.

Source of variation	SS	df	MS	Approx. F	MLR[a]
Regression	77.7498	5	15.54	95.55	4.33×10^{-34}
Linear	3.1974	2	1.59	9.82	5.70×10^{-5}
x_1	1.7331	1	1.73	10.64	3.60×10^{-3}
x_2	0.5732	1	0.57	3.52	0.141
Quadratic	66.2872	2	33.14	203.66	6.20×10^{-32}
x_1^2	3.2259	1	3.22	19.82	5.28×10^{-5}
x_2^2	63.4623	1	63.46	389.96	2.36×10^{-31}
Interaction					
$x_1 * x_2$	14.7004	1	14.70	90.33	1.38×10^{-14}
Transform	21.8571	3	7.28	44.76	1.70×10^{-18}
Residual	10.0898	62	0.16	–	–
Total	87.8397	70	–	–	–

[a]True F ratios cannot be calculated from the transformed data, whereas exact inferences are available by maximum likelihood procedure. Maximum likelihood ratios give the maximized relative likelihood of a coefficient parameter being zero, or of a power parameter being unity. For a given parameter, a high MLR value indicates that the parameter may be eliminated without greatly affecting the adequacy of the model. MLR values >0.1 may be compared with a 95% probability interval for a normal theory linear model (Lindsey et al. 1970; Lindsey and Sandnes MS 1970).

In the latter, the level of performance calculated over most of the ridge probably could not be distinguished in these tests from the level of performance to be expected on the axis of equal acclimation and test temperatures (solid diagonal line, Fig. 3). Nevertheless, the results indicate that with regard to acclimation and acute temperature experience, performance is maximal on the two ridge systems which culminate in optimum performance at their intersection at the centre of the surface.

Second Series

This series of tests was conducted between January 30 and April 11, 1969 (Fig. 4). The data were subjected to response surface analysis in the same manner as the first series. Hence

$$Y^{2.48} = 2.065 + 12.252x_1^{0.56} + 0.121x_2^{2.18} - 2.213x_1^{1.12} - 1.6 \times 10^{-4}x_2^{4.36} + 0.018x_1^{0.56}x_2^{2.18}$$

where $\alpha_1, \alpha_2, \gamma = 0.564, 2.177, 2.476$

The relative likelihood of a linear model providing an adequate fit to the data, compared with the non-linear model employed, is 2.99×10^{-10}, or nearly zero.

Variance is partitioned into components (Table 2) as for the first series of performance tests. None of the components could be omitted from the regression equation without seriously affecting the adequacy of the model.

The response surface is constructed (Fig. 5) relating critical swimming speed to levels of acclimation

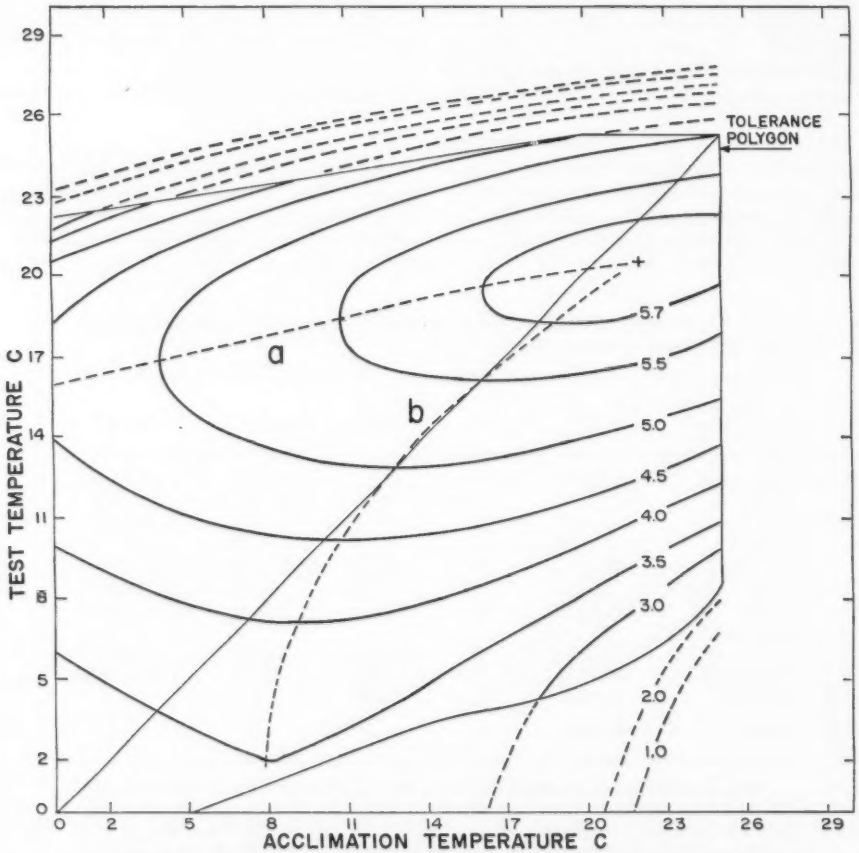

FIG. 3. Isopleths of critical swimming speed (L/sec) calculated for the first test series. Axes of the surface are defined as (a) test-temperature and (b) acclimation-temperature ridges of maximum performance (see text). The zone of thermal tolerance is that defined by Brett (1952).

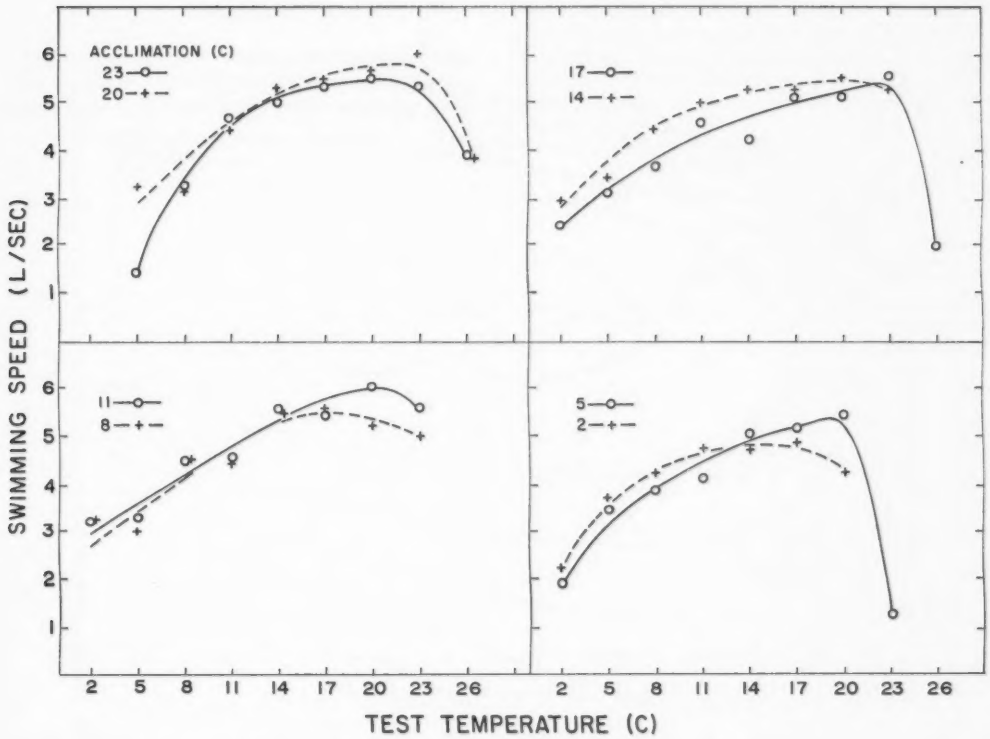

FIG. 4. Critical swimming speeds of young coho salmon (L/sec) determined acutely for temperatures between 2 and 26 C. Curves eye-fitted. Second series.

TABLE 2. Analysis of variance of the data for the second series of tests according to the nonlinear model.

Source of variation	SS	df	MS	Approx. F	MLR[a]
Regression	63.4825	5	12.69	53.00	3.36×10^{-25}
Linear	11.7187	2	5.85	24.46	1.44×10^{-9}
x_1	1.7654	1	1.77	7.37	1.79×10^{-2}
x_2	7.4766	1	7.48	31.21	5.67×10^{-7}
Quadratic	46.6719	2	23.33	97.42	9.26×10^{-22}
x_1^2	2.2866	1	2.29	9.54	5.97×10^{-3}
x_2^2	45.5843	1	45.58	190.30	1.66×10^{-21}
Interaction					
$x_1 * x_2$	7.3476	1	7.35	30.67	6.93×10^{-7}
Transform	12.9710	3	4.32	18.04	2.98×10^{-10}
Residual	13.1746	55	0.23	–	–
Total	76.6571	63	–	–	–

[a]See explanation, Table 1.

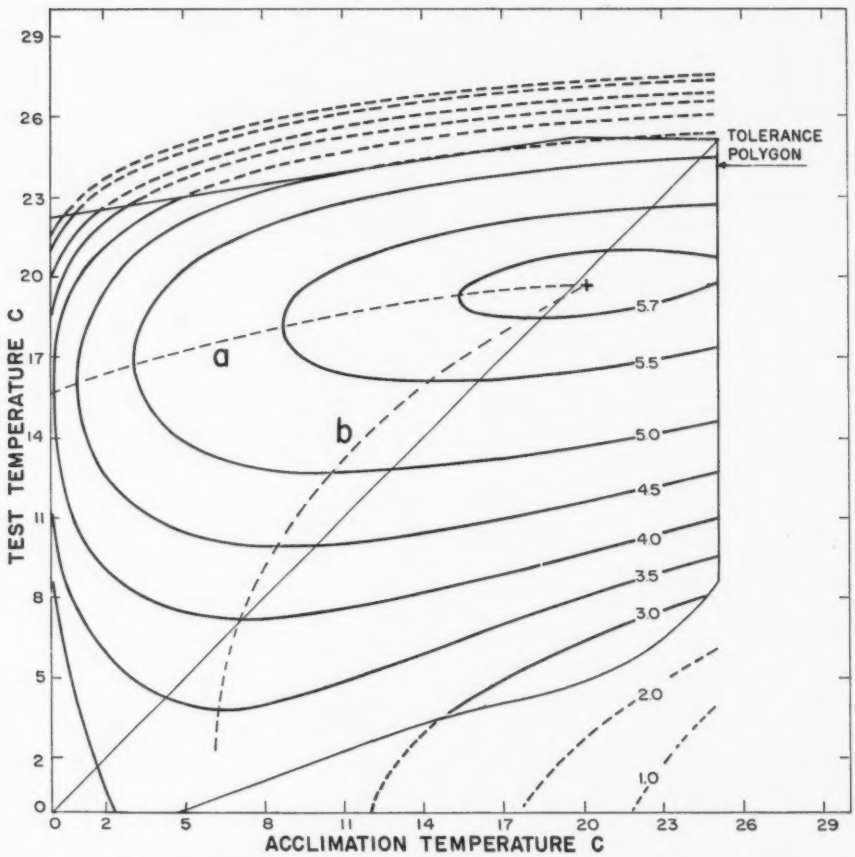

FIG. 5. Isopleths of critical swimming speed (L/sec) calculated for the second test series. Axes (a) and (b) are as defined for Fig. 3.

and test temperature. The canonical equation of the surface is:

$$Y' - 75.370 = -2.213Z_1^2 - 0.00013Z_2^2$$

where Y' = critical swimming speed in terms of Y^{γ}

$75.370 = Y_s^{\gamma}$, swimming speed at the centre of the surface, S

Z_1, Z_2 = canonical variables.

As in the first series, the surface is a modified ellipse with a maximum at the centre. Transposed to original units, the response at the centre of the surface is 5.73 L/sec, calculated to occur at:

S = (acclimation temperature 20.15 C; test temperature 19.71 C).

Some of the data from which the two swimming speed surfaces were constructed (Fig. 3, 5) are shown as transects of those surfaces at acclimation temperatures of 2, 8, 14, 20, and 23 C (Fig. 6), and at test temperatures of 2, 8, 14, 20, 23, and 26 C (Fig. 7). The transects indicate the general trends in swimming capacity over the temperature surfaces; those at 5, 11, and 17 C were omitted to reduce complexity of the figures. The scales employed are those indicated by the analyses. Hence swimming speed is scaled for each series in terms of γlnY lengths/sec, while acclimation and test temperatures are scaled in terms of $\alpha_1 lnx_1$ (C) and $\alpha_2 lnx_2$ (C), respectively.

Discussion

The exploration of multifactor biological relations presents a number of challenges. Biological relations, such as those examined here, appear largely to be nonlinear, and the linear scales the investigator normally uses to examine them could be said to have little "meaning" to the organisms or systems investigated. The complexity of design and analysis increases rapidly with the addition of further envi-

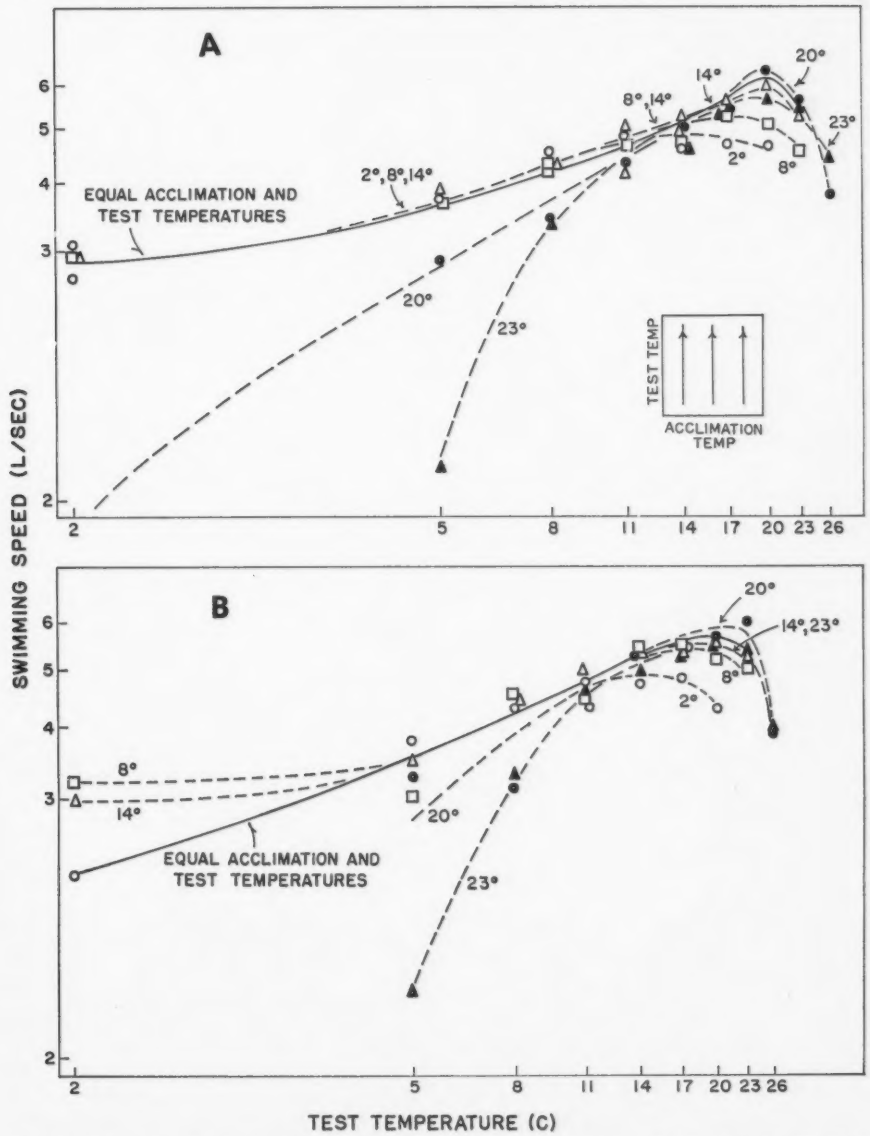

FIG. 6. Transects of swimming-speed surfaces at acclimation temperature levels 2, 8, 14, 20, 23 C. Direction of transects shown in inset. A, transects of Fig. 3 (first test series); B, transects of Fig. 5 (second test series).

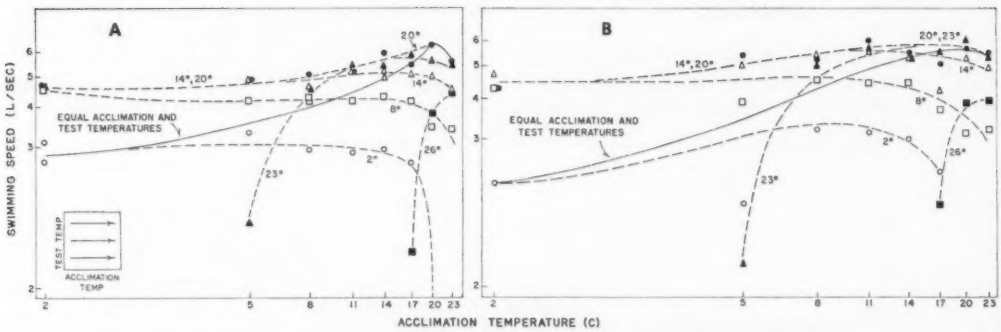

FIG. 7. Transects of swimming-speed surfaces at test temperature levels 2, 8, 14, 20, 23, 26 C. Direction of transects shown in inset. A, transects of Fig. 3 (first test series); B, transects of Fig. 5 (second test series).

ronmental variables, and the time required for investigation increases proportionally. Conversely, there is a need to compress time into short intervals, in order to sample attributes of the experimental animal at given periods in its physiological age. However, the use of simpler designs and correspondingly reduced numbers of sample points may reduce chances of sampling important portions of the test space under study. Increased replication at each sample point leads to improved estimates of response at each point; conversely, increased experimental time introduces the possibility of a progressive bias occurring over the test space as response changes in relation to changing size or physiological age of the test animal.

For these reasons, the best experimental approach was considered to be the determination of swimming speeds from measures of central tendency in single samples taken at as many loci in the temperature space as time would permit. The calculated swimming-speed surfaces are considered as estimates of the true nature of the temperature-performance relation, given the data and the regression model. The data are discussed from this point of view.

EFFECTS OF TEST TEMPERATURE ON PERFORMANCE

The five acclimation temperature transects of the performance surface (Fig. 6) demonstrate a progressive shift in their maxima toward higher test temperatures as acclimation increases from 2 to approximately 20 C. At an acclimation temperature of 23 C, the performance maximum appears to remain near 20 C or to regress to slightly lower test temperatures. Comparison of these transects with the surfaces of Fig. 3 and 5 shows the performance maxima to be located on the upper performance ridge (axis *a*). Performance on this ridge may be considered as a function of test (acute) temperature, the location of the maxima being modified by acclimation temperature experience. The ridge is that which would be seen if the surface was viewed "end-on" from the test temperature axis. It may be defined as the ridge locating those test temperatures which maximize performance at given acclimation temperatures. Therefore, it is referred to as the test temperature ridge of maximum performance, or the *test temperature ridge*.

If the test temperature ridge were parallel to the acclimation temperature axis, the action of both acclimation and test temperature would be judged as independent in their effects on performance. Instead there is an interaction between acclimation and test temperature (see Tables 1, 2); at higher acclimation temperatures, maximum performance is found on the ridge at higher acute temperature levels. The discrepancy between the two temperatures decreases until the centre for optimum activity is reached near 20 C. The position of the test temperature ridge also leads to the conclusion that the coho's capacity for activity, over much of the zone of thermal tolerance, is greatest at environmental temperatures considerably higher than those to which it may be acclimated.

EFFECTS OF ACCLIMATION TEMPERATURE ON PERFORMANCE

The six test-temperature transects of the performance surface (Fig. 7) show a progressive shift in their maxima toward higher acclimation temperatures as test temperatures increase from 2 to approximately 20 C. The performance curves at each test temperature are quite flat, indicating that the level of performance attained at each test temperature is fairly constant between acclimation temperatures of 2 and 17–20 C. Comparing the transects of Fig. 7 with the surfaces they represent (Figs. 3, 5) shows that the performance maxima of the former, as well as they may be determined, are located on the lower

performance ridge (axis *b*). By reasoning similar to that in the previous section, this axis may be defined as the ridge locating those acclimation temperatures which maximize performance at given test temperatures. Therefore, it is referred to as the acclimation temperature ridge of maximum performance, or *acclimation temperature ridge*. In Fig. 7 the maxima are not well defined. More confidence is placed in the determination of the acclimation temperature ridge joining these maxima (Fig. 3, 5), as the ridge is defined by regression using all available data.

Figure 7 shows that a large portion of each temperature transect is not well sampled (between 2 and 5 C) by the linear set of experimental temperatures employed. There is limited curvature to the swimming-speed isopleths at acclimation temperatures from about 2–8 C. It is desirable to know more precisely the location of the acclimation temperature ridge in this region. As performance does not change appreciably when crossing the acclimation temperature ridge, the frequency of sampling should be increased by the addition of further acclimation temperatures below 8 C. The same argument applies to the need for additional test-temperature transects below 8 C. In fact the performance surfaces, as illustrated, indicate the need for an orthogonal design of acclimation- and test-temperature sampling points in the scales determined by the analyses. A minimum approximation to these requirements would be the addition of further sampling points to both acclimation- and test-temperature series at about 3, 4, and 6.5 C.

On the basis of considerable evidence of the nature shown in Fig. 6, Fry (1967 p. 393) concludes that "at a given temperature, the animal performs at its best when acclimated to that temperature." Performance at such equal acclimation- and test-temperature conditions is shown by the solid curve in Fig. 6. In general, Fry's conclusion is substantiated by the data on coho salmon performance between temperatures of 5 and 20 C. Outside this range there is some uncertainty in the predicted relation. For example, at a given test temperature of 2 C (Fig. 6B) the coho salmon appears to perform best when acclimated to temperatures higher than 2 C. At a test temperature of 23 C, best performance appears to occur at acclimation temperatures of 17–20 C (Fig. 7). Fry's conclusion is equivalent to stating that maximum performance will be found on the equal acclimation, test-temperature diagonal (Fig. 3, 5), whereas the present data indicate that it occurs on the acclimation temperature ridge. Over most of the temperature range investigated, however, performance at a given test temperature, whether measured on the diagonal or on the acclimation temperature ridge, lies within the 0.4 L/sec error estimate associated with position of the isopleths. Therefore further examination of the question for young coho salmon would be assisted by description of the temperature of maximum swimming capacity over a series of acclimation temperatures, but at test temperatures above the performance centre (23–25 C), near 2 C.

Comparison of Performance Surfaces

Comparison of the swimming speed surfaces for the series conducted in the fall and winter months (Fig. 3), and in late winter and early spring (Fig. 5), shows the surfaces to be similar but not identical. Compared at specific temperature loci, differences in performance in a number of instances are larger than the initial estimate of experimental error (0.4 L/sec). Differences between the two surfaces could be real, and they are examined from this point of view.

The maximum likelihood estimates of the α_1, α_2, γ power parameters in each surface equation are the most plausible values from the set of possible estimates for each parameter (Fig. 8). As a means of comparing the two surfaces, the relative likelihood (R) of each set of maximum likelihood estimates of the power parameters may be compared, as alternative solutions, with those calculated for the other series. Hence the estimates calculated for the first series of tests are plausible, although borderline, alternatives for the corresponding parameters in the second series (R ($\alpha_1 = 1.161$, $\alpha_2 = 2.352$, $\gamma = 2.371$) = 0.12) (see footnote, Table 1). Conversely, estimates for the second series are unlikely alternatives for the first series (R ($\alpha_1 = 0.564$, $\alpha_2 = 2.177$, $\gamma = 2.476$) = 0.04). On this basis, it is suspected that the differences between the two swimming-speed surfaces are real although small in magnitude.

Location of the test temperature ridge is substantially the same in the two test series. However there is a shift in the position of the acclimation temperature ridge (Fig. 3) toward lower acclimation temperatures (Fig. 5). The shift is also indicated in the reduction of acclimation and test temperatures at the surface centre from (22.03 C, 20.45 C) in the first series, to (20.15 C, 19.17 C) in the second. In spite of the apparent shift of the acclimation temperature ridge, maximum performance over most of the ridge remains nearly constant. Hence the surfaces indicate that *acclimation temperature of maximum performance shifts to lower acclimation temperatures* between fall and early winter, and late winter and early spring, while the *capacity to perform under those conditions remains relatively constant.* Since the comparison is made between acclimated fish, differences in location of the acclimation tempera-

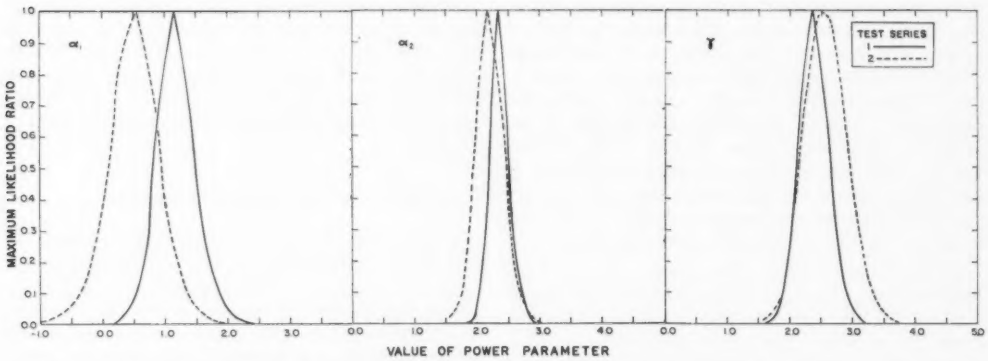

FIG. 8. Relative likelihood of other values of the α_1, α_2, γ power parameters around their maximum likelihood estimates for each of the two test series.

ture ridge suggest that a form of *performance compensation* occurs, associated with seasonal differences in physiological state. Such compensation would allow the coho to perform at maximum capacity in late winter, at acclimation temperatures 1–3 C below those providing maximum swimming capacity in the fall and early winter.

Although the two series of swimming-speed trials have not been pooled, it is of interest to consider "averaging" the differences between the power parameters of their surface equations. Taking the value of each power parameter for each series at the point of intersection of their likelihood distributions (Fig. 8) yields approximately the following set whose relative likelihood, with respect to the maximum likelihood estimates of each series, is about $R(\alpha_1 = 0.88, \alpha_2 = 2.3, \gamma = 2.4) = 0.50$. In general, the relation between critical swimming speed and acclimation and test temperature for young coho salmon 7–9 cm in total length may be approximated by

$$Y^{2.4} = b_0x_0 + b_1x_1^{0.88} + b_2x_2^{2.3} - b_{11}x_1^{1.76} - b_{22}x_2^{4.6} + b_{12}x_1^{0.88}x_2^{2.3}$$

Location of the centre of the surface in each series is also dependent in part on the estimates of the power parameters employed. The plausibility of other estimates of the surface centres is shown in Fig. 9. "Average" values for the surface centre may be read from the graphs, at the point of intersection of the two distributions for acclimation and test temperature, as (21.5 C, 20.0 C). The distributions also indicate that the centre point for test temperature is estimated with more precision than that for acclimation temperature. This is presumed to result from the fact that changes in slope on the surface are great-

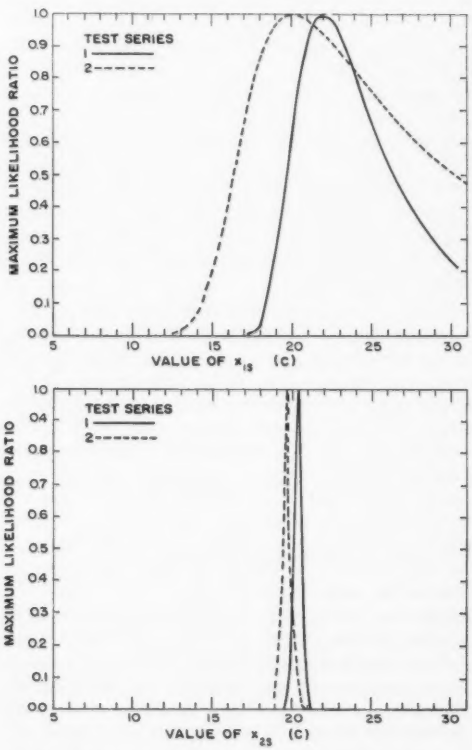

FIG. 9. Relative likelihood of other levels of acclimation (x_{1s}) and test (x_{2s}) temperature at the centre of the performance surface in each of the two test series, as compared with maximum likelihood values calculated in the text.

er in the direction of the test temperature axis (Fig. 6) than in the direction of the acclimation temperature axis (Fig. 7). For example, isopleths are elongated at the centre of the surface in the direction of the acclimation temperature axis, when compared with the greater curvature shown in the direction of the test temperature axis (e.g. Fig. 5, 5.7 L/sec isopleth). Greater curvature, compared with errors of estimation, would lead to a more restricted definition of test temperature at the surface centre (as well as on the test temperature ridge).

Ecological Implications

Young coho salmon are well adapted to maintaining a high level of swimming performance over a broad range of temperature experience. Maximum capacity to swim at 2 C differs only by a factor of 2 from that achieved at 20 C. In fact, within the temperature tolerance polygon of the coho salmon (Fig. 3, 5), temperature experience allowing at least 50% of ultimate maximum swimming capacity (i.e., 3 L/sec) is seen to include most of the zone of thermal tolerance. This range of temperature-dependent performance is consistent with the habitat of young coho salmon. They may be found at the height of summer water temperatures in rivers draining eutrophic lakes, and in the warm, shallow littoral regions of those lakes (Brett et al. 1958). In addition they are found in cold water streams and overwinter in bottom detritus of streams when water temperatures drop to annual minima (Neate 1968).

Discussion of the relation between temperature and aspects of swimming capacity are aided by a comparison with the considerable data available on temperature-dependent physiological parameters in sockeye salmon (*O. nerka*) (Brett 1971). Juvenile sockeye salmon characteristically inhabit the limnetic region of lakes, and very often occupy the same water system as young coho salmon. Juvenile sockeye salmon perform diurnal vertical feeding migrations, but occupy the colder, deeper water of the lake for the greater portion of a 24-hr period. In contrast, trawling operations in these open waters have found no juvenile coho salmon in association with sockeye salmon (Johnson 1956; Narver 1970).

Brett (1971) shows that a number of parameters in sockeye salmon, among them maximum swimming capacity, metabolic scope, growth on excess rations, and appetite (voluntary food intake) are maximized at 15 C, which also is the preferred temperature of the species. There is an interaction between food availability (ration) and temperature; maximum growth on excess rations occurs at 15 C, while gross conversion efficiency is maximized at 11.5 C. Both maxima occur on a "favorable axis", a ridge running from about 5 to 15 C. Hence for the sockeye salmon there has evolved, relative to a number of interdependent factors, a "pattern of thermoregulation peculiarly adapted to maximizing growth, through the selective pressure of bioenergetic efficiency" (Brett 1971). The ultimate maximum in this multivariate relationship occurs at 15 C, which in this sense is considered an *optimum* temperature for sockeye salmon.

Less information related to temperature optima is available for young coho salmon. Maximum swimming speeds are found near 20 C. Maximum growth on excess rations occurs in the region of 17–20 C, while food conversion is most efficient at lower temperatures: 5–14 C, early spring; 11–14 C, early summer; 14–17 C, late summer; 11–17 C, fall; 5–8 C, late winter (Averett MS 1969). It appears that swimming speed, conversion efficiency, and growth in young coho salmon are associated in a manner similar to that found for sockeye salmon. Hence a physiological optimum, comparable to that of sockeye salmon, is presumed to occur near 20 C in young coho salmon.

If such is the case, differences in habitat temperatures of the two species are reflected by their temperature optima. However, judgements concerning ecological significance of these optima are seen primarily to depend on an understanding of the interrelations between the parameters which determine the optima. For the coho salmon it appears that 20 C may provide maximum metabolic scope, hence maximum swimming speed, maximum food-gathering capacity, and maximum growth, as long as food availability is not a limiting factor. Conversely, it is presumed that the degree of spacial or temporal exploitation of optimum temperature conditions may be directly related to food availability relative to satiation levels.

Acknowledgments

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Comparative Behavior and Habitat Utilization of Brook Trout (*Salvelinus fontinalis*) and Cutthroat Trout (*Salmo clarki*) in Small Streams in Northern Idaho

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Individual brook (*Salvelinus fontinalis*) and cutthroat (*Salmo clarki*) trout communicated with similar behavioral signals, both in laboratory stream-channels and in northern Idaho streams. Underyearling brook trout were less active socially than equal-sized cutthroat trout in laboratory observations. In study streams, brook trout maintained a 20-mm size advantage over cutthroat of the same age-groups throughout their lives, as they emerged from the gravel before cutthroat. Because of this size advantage, underyearling brook trout of sizes found in study streams in September consistently dominated in experiments the underyearling cutthroat with which they normally lived. But in study streams underyearlings of the two species utilized different microhabitats, particularly with respect to water depth, and so minimized chances for interaction.

Yearling and older brook trout initiated 40% fewer aggressive encounters under laboratory conditions than did equal-sized cutthroat trout, and did not displace the cutthroat. In study streams with sympatric populations, cutthroat trout of these age-groups occupied territories with focal points of higher water velocities (averaging 10.2–10.3 cm/sec) than those occupied by brook trout (averaging 7.6–9.6 cm/sec). Considerable interspecific overlap in other habitat characteristics occurred for trout of age-groups I and II. The oldest members of the two species segregated more distinctly, as the brook trout lived closer to overhead cover.

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Des ombles de fontaine (*Salvelinus fontinalis*) et des truites cutthroat (*Salmo clarki*) observés au laboratoire dans des viviers à eau courante et dans des cours d'eau du nord de l'Idaho, communiquent entre eux par un comportement de signaux semblables. Au laboratoire, les ombles de fontaine de moins d'un an sont socialement moins actifs que les truites cutthroat de même taille. Parce qu'ils émergent plus tôt du gravier des cours d'eau sous étude, les ombles de fontaine maintiennent durant toute leur vie une avance de 20 mm en longueur sur les truites cutthroat du même groupe d'âge. Pour cette raison, les ombles de fontaine de moins d'un an, qui ont atteint la taille observée en septembre dans les cours d'eau étudiés, dominent infailliblement les truites cutthroat du même âge. Dans ces cours d'eau, toutefois, les deux espèces occupent des microhabitats différents, ce qui minimise les chances d'interaction.

Au laboratoire, les ombles de fontaine d'un an ou plus sont la cause, dans une proportion de 40%, de moins de rencontres agressives que les truites cutthroat qu'ils ne dominent d'ailleurs pas. Dans les cours d'eau sous étude où vivent des populations sympatriques, les truites cutthroat de ces groupes d'âge occupent des territoires à courant plus fort au point focal (10.2 à 10.3 cm/sec en moyenne) que ceux occupés par les ombles de fontaine (7.6 à 9.6 cm/sec en moyenne). Chez les truites de groupes d'âge I et II, il y a chevauchement interspécifique considérable des autres caractéristiques du milieu. Comme les ombles de fontaine se tiennent plus près des abris d'en-dessus que les truites cutthroat, il y a ségrégation plus marquée entre les plus vieux individus des deux espèces.

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CUTTHROAT trout (*Salmo clarki*) have shared much of their range in the Rocky Mountains with brook trout (*Salvelinus fontinalis*) since the initial introduction of the latter 75 years ago (Bean 1894). Cutthroat have steadily declined in abundance, while in some areas the density of brook trout has increased (Hanzel 1959; Domrose 1963).

I studied interspecific interaction in this unnatural sympatry to assess its role in the decline in cutthroat trout numbers. Brook trout may actively displace cutthroat trout, or may replace a population of cutthroat depressed in numbers by other factors. The possibility of active displacement was evaluated by examining behavior of the two species in stream-channels at the University of Idaho to assess whether members of the two species communicate with similar behavioral signals, and if they do, whether brook trout are more socially active than cutthroat trout and thus gain a behavioral advantage. Also, I examined summer habitat utilization by each of the species, living together and separately, in four northern Idaho streams during 1968 and 1969 to assess the development of habitat segregation that may act to minimize interaction.

Laboratory Procedures

Two sets of experiments were conducted in separate stream-channels to study trout behavior: one for fish not more than 80 mm long and the other for those 100–175 mm long. Groups of the small brook and cutthroat trout of equal sizes, and of sizes representative of those found in study streams in September, were studied allopatrically and sympatrically in 1968–69 to examine behavioral differences. Matched pairs of the larger trout were observed in sympatric trials during 1969–70 to assess interspecific differences and the effects of prior residence.

SMALL TROUT

The ring-shaped recirculating channel, designed to simulate the portions of northern Idaho streams inhabited by underyearling trout, was previously described by Edmundson et al. (1968). It was 0.6–m wide, 0.5–m deep, and 12-m long. Water depth was constant at 30 cm except for a riffle 15-cm deep and 80-cm long, and water velocities, 8–9 cm/sec in most areas, ranged from 0 to 13 cm/sec. Two 95-liter/min pumps circulated water, and a third forced food through a perforated pipe laid in the substrate of gravel, sand, and rock. Two floating pieces of plywood provided overhead cover.

A cooling system maintained temperatures at 10 C. A timer gradually dimmed and brightened incandescent lights for a 9-hr day (0800–1700 hr Pacific Standard Time). An amount of frozen brine shrimp (*Artemia salina*), corresponding to 10% of the total biomass of trout being fed, was released daily into the channel at seven random times each hour from 0800 to 1800 hr.

For experiments in 1968, 18 fish of each species between 60 and 80 mm were selected from groups collected by electrofishing in Pack and Deer Creeks in November. Brook trout, all underyearlings, averaged 69-mm long, while cutthroat, all yearlings, averaged 70 mm. In September of 1969 I collected 18 fish of each species, of sizes representing lengths of underyearling trout in the stream at that time. Cutthroat trout ranged from 32- to 50-mm long with a mean of 44 mm, and brook trout ranged from 52- to 72-mm long with a mean of 63 mm.

Members of each species were held in separate 1600-liter tanks at 10 C until experiments began on November 12, 1968, and December 2, 1969. Each year, members of each species were observed separately for 8 days, netted from the channel and held 1 day, and then placed together in the channel for 8 days. During the first day of each trial, fish that left the channel through a downstream trap were placed back upstream; subsequent emigrants were removed. Observations began on the morning of the second day of the trial, with three observation periods (0800–0900, 1200–1300, and 1500–1600 hr) daily for 7 days.

During each period five fish were observed. As their small size precluded identification of individuals, I assigned each a number corresponding to its position in the channel and randomly selected five of the numbers. I watched each trout for 2 min and recorded the number of lateral and frontal threats, nips, nips-close (same as threat-nips of Hartman 1965), and drives (same as chases of Hartman 1965) initiated by the observed fish only.

LARGE TROUT

Two plywood and fiberglass stream-channels sharing a common water recirculation system (Fig. 1) were constructed to simulate the dimensions, water velocity, and substrate of pools in the study streams. Each channel contained four pools, each 1.3-m wide: two 1.0-m deep and 2.6-m long, one 0.3-m deep and 1.3-m long, and one 0.6-m deep and 2.6-m long. Plexiglass windows in each of the darkened observation chambers allowed surveillance of all areas. Fish could emigrate by moving with the flow of water, 30 mm deep, over the end of each channel into a trap.

A cooling system maintained water temperatures at 10–14 C. Photoperiod and feeding procedures were the same as those for the small fish except that amphipods (*Gammarus* sp.) served as food instead of brine shrimp. The feeder released equal quantities of food to the two channels. Branches of conifers and willows provided overhead cover, and floating planks simulated undercut banks. Gravel with small amounts of sand and rock, and sand with some silt comprised the substrates of channels A and B, respectively. Four 95-liter/min pumps in channel A, and three in channel B circulated water, and another increased water velocity in the intermediate-depth area of each channel. Water velocity was approximately 21 cm/sec at the heads of the upper pools and intermediate areas, 11 cm/sec in the shallow shelves, and 8 cm/sec in the lower pools.

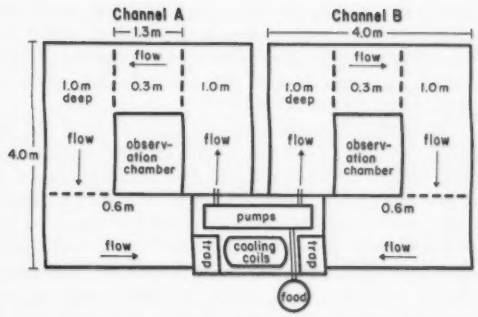

FIG. 1. Schematic plan of set of 2 stream-channels for observation of 100-mm and larger trout at the University of Idaho. Perforated pipes buried in substrate supplied food.

Brook and cutthroat trout were collected by electrofishing in Pack and Deer Creeks during October of 1969, and held separately until their use from December 23, 1969, to April 11, 1970. Four groups of 10 fish were selected, each group consisting of one brook and one cutthroat trout of equal length (to the nearest mm) in each 15-mm size interval from 100 to 175 mm. In the first and second trials (which ran concurrently) one group was placed in each channel. For 10 days fish that emigrated were placed back upstream; if a fish left twice during this period or once afterward, it was not replaced. For the next 10 days two brook and two cutthroat trout in each channel were randomly selected and observed for periods of 4 min beginning at 0900 and 1500 hr daily. The numbers of lateral and frontal threats, nips, nips-close, and drives initiated by and against the observed trout were recorded.

On the twenty-first day, I removed all trout by electrofishing and placed the group from channel A into channel B for the third trial, and the group from channel B into channel A for the fourth trial. After 5 days the fish were observed as before for 5 days and removed. The remaining two groups were then observed in the same manner in four more trials.

The effect of prior residence was tested with four groups of 10 fish, matched as before, from March 22 to April 11, 1970. I allowed the brook trout of the first group to become established in channel A, and the cutthroat of the second group to become established in channel B for 2 days. Members of the other species of each group were then held in a 30-liter perforated plastic container partially submerged in each stream-channel. After 13 hr, a door in the container was opened to allow them to enter the channel without disturbance. I alternated 15-min observation periods between channels for 8 hr to record behavioral encounters and emigration. This procedure was then repeated with the other two groups of fish, except that cutthroat were allowed prior residence in channel A, and brook trout in channel B.

Field Sites and Procedures

The four study streams drain into the Clearwater River, a tributary of the Snake River (Fig. 2). They ranged from 5–8 m in maximum width, 0.8-1.2 m in maximum depth, and 0.06-0.10 m^3/sec in minimum flow within the 1 km-long study sections.

Cutthroat trout, originally present in all streams, alone inhabited the study area in Pack Creek at time of sampling in 1968-69. The naturally reproducing population had been unaltered by stocking. Brook trout, the only species living in the portion of Deer Creek studied, were stocked there from 1940 to 1949. Both species inhabited Hoodoo and Crystal Creeks. In Hoodoo Creek, brook trout were the progeny of emigrants from lake plantings in 1940–50. Cutthroat were stocked occasionally in the stream until 1961. The brook trout present in Crystal Creek presumably originated from a release in 1948 in a tributary of Orogrande Creek, 12 km distant; no brook trout lived in Crystal Creek in 1956 (Oien MS 1957). Plantings of cutthroat through 1948 supplemented the native population of that species.

A few rainbow trout (*Salmo gairdneri*) below study sections in each stream represented the only other species present.

Each stream was electrofished semi-monthly from mid-June through September, 1969. Scales from each of the 318 brook and 221 cutthroat trout collected were examined to assess ages.

To study interaction for physical habitat between species, I located individual fish while swimming with mask and snorkel, noted their exact locations, and killed them to accurately assess size and age. In the four streams,

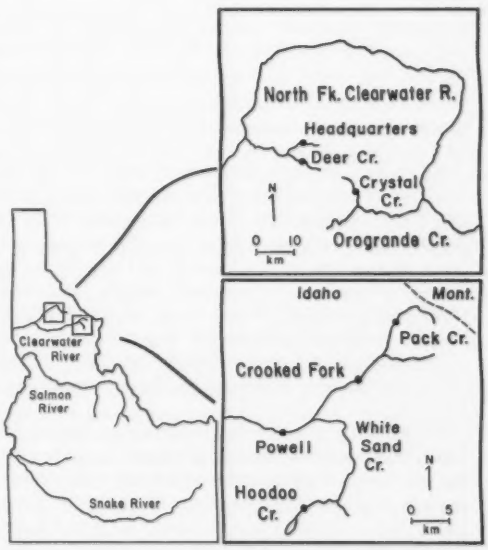

FIG. 2. Location of study areas on Hoodoo, Pack, Crystal, and Deer creeks, Idaho.

93 brook and 113 cutthroat trout of all age-groups present were collected in this manner, half in August, 1968, and half in August, 1969. To ensure maximum visibility, diving was done only on sunny days, between 1000 and 1600 hr (Pacific Daylight Time). I swam upstream from a predetermined starting point until a trout of the age and species desired that showed no indication of alarm or displacement was noted. After watching for 2–3 min to ascertain its focal point, or center of territorial and feeding activity, I killed the fish with a gun which fired an electric blasting cap under water (Everest MS 1969), and marked the focal point. Distance to overhead cover, water velocity and depth, substrate composition at the focal point, and maximum water velocity within 0.3 m for underyearlings and within 0.6 m for older trout were recorded. Current velocities were measured to the nearest centimeter per second with midget Bentzel current speed tubes (Everest 1967). Substrate was classified as silt, sand, gravel (2–10-cm diameter), and rock (> 10-cm diameter). Overhanging brush and logs and undercut banks constituted cover for fish of age-group I and older; for underyearlings aquatic vegetation was also included. After completing measurements for one fish, I walked up the stream bank a number of paces from 1 to 30, predetermined from a random number table, then entered the water to seek the next fish.

Mean focal point characteristics were compared between age-groups and between species for trout living sympatrically and allopatrically.

Laboratory Observations

Small Trout

Behavior patterns — After introduction of each group into the stream-channel, one or more clusters of 4–15 fish spent several hours exploring channel boundaries. Other individuals remained in one location, and began to feed and exhibit aggression within minutes.

Approximately half the trout of each species held territories against equal-sized and smaller fish. Dominant trout maintained focal points near areas of higher water velocity behind the riffle section and behind piles of rock. A maximum of four fish in any group of either or both species, usually the largest individuals, defended large areas. Other trout remained in general areas but not at specific focal points, and formed a dominance hierarchy. Neither species displayed a preference for the overhead cover provided.

Members of each species responded to the other's behavioral signals. Juvenile cutthroat trout carried out aggressive actions more elaborately, occasionally rushing at an opponent from 20 cm away, slamming against it and nipping its dorsal fin area. Underyearling brook trout exhibited lateral displays in a less vigorous manner, and chased opponents more slowly. Subordinate brook trout often wedged themselves between rocks, or if rocks were not available, in corners on the bottom, and remained there for extended periods. Subordinate cutthroat trout sought refuge along the edge of the channel a few centimeters below the water surface.

In every allopatric trial but one, 7–8 of the 18 trout introduced left the stream-channel during the first 3 days of observation, after which population sizes stabilized. In one case, 15 brook trout remained in the channel, but several of these lay on the bottom in pool areas without feeding or interacting with others. A total of 20 trout of both species, about twice that from allopatric trials, remained at the end of each sympatric trial; 12 brook and 8 cutthroat trout when members of the two species averaged the same length in 1968, and 14 brook and 6 cutthroat trout when brook trout were longer in 1969.

Frequencies of encounters — In experiments with groups of each species averaging the same length, allopatric cutthroat trout were about twice as active as brook trout in most types of agonistic activity (Table 1). When members of the two species were placed in the channel together, the cutthroat trout maintained a higher level of aggression by initiating a total of 64 offensive encounters (all activities except lateral threats, which were usually defensive in nature) toward members of the two species, compared with 41 initiated by brook trout. Cutthroat trout directed over two-thirds of their offensive activity toward brook trout, and brook trout directed two-thirds of their offensive encounters toward other brook trout, indicating that the species were equally aggressive toward each other since four more brook trout than cutthroat trout remained in the channel.

When brook trout averaged 20 mm longer than cutthroat trout, cutthroat trout continued to be more active in allopatry than brook trout (Table 1). A shift in frequencies occurred in sympatric populations. Cutthroat trout now initiated only six offensive encounters toward brook trout, less than one-seventh of the number initiated when the species were equal in length. Since only six of the 20 trout present were cutthroat, this indicates that cutthroat trout were more likely to attack other cutthroat trout ($X^2 = 35.32$, $P < .005$). Similarly, the brook trout in this trial were more likely to attack the smaller cutthroat trout ($X^2 = 31.80$, $P < .005$).

Large Trout

Behavior patterns — When introduced into the channels, most of the brook trout immediately swam to the channel bottom and remained there up to 1 hr before moving. Cutthroat trout quickly began to investigate channel boundaries and to feed and

TABLE 1. Numbers of agonistic acts initiated per allopatric and sympatric observation period[a], and totals of offensive acts (all acts except lateral threats) initiated by cutthroat and brook trout in the small stream-channel, 1968–69. Initially 18 fish of each species.

Species	Lateral threats	Frontal threats	Nips	Nips-close	Drives	Total
Equal in length[b] *(1968)*						
			Allopatric			
Brook	24	4	14	7	11	36
Cutthroat	13	8	17	16	27	68
			Sympatric			
Brook–brook[d]	11	3	10	7	7	27
Brook–cutthroat	2	3	4	3	4	14
Cutthroat–cutthroat	3	0	2	8	10	20
Cutthroat–brook	15	7	15	11	11	44
Brook Trout Larger[c] *(1969)*						
			Allopatric			
Brook	3	3	11	2	5	21
Cutthroat	5	0	16	6	4	26
			Sympatric			
Brook–brook	4	0	9	0	6	15
Brook–cutthroat	2	0	15	3	10	28
Cutthroat–cutthroat	4	0	5	5	11	21
Cutthroat–brook	4	0	6	0	0	6

[a]Observation period for each species 105 min in allopatric trials; sympatric trials 210 min.
[b]Both species 60–80 mm.
[c]Cutthroat 32–50 mm, brook trout 52–72 mm.
[d]First species initiator, second species recipient of act.

exhibit aggression. Neither species showed evidence of schooling behavior. Three cutthroat and two brook trout left the channels during observation periods and could not be observed for totals of 12 and 16 fish-days, respectively. Because this emigration remained approximately equal for the two species, quantitative data were not adjusted.

Each species responded to the other's behavioral signals, and I detected no qualitative interspecific differences in the patterns observed except that escape and avoidance movements differed between species in the same manner as they had for small trout. Behavior seemed the same in the two stream-channels.

Between two and five of the 10 trout in each channel defended territories in each trial. Seven brook and 19 cutthroat trout held territories for totals of 48 and 143 fish-days, respectively, at the heads of the two deep pools, the shallow shelf, and the area of intermediate depth near the water-circulating pump in each channel. Only trout defending the shallow shelf remained at distinct focal points. Territorial fish holding the other areas patrolled their territories and investigated other parts of the channel, forming a dominance hierarchy with non-territorial trout. In every trial the largest or second-largest cutthroat occupied the head of each uppermost pool, holding in swift water 30 cm or more above the substrate. During four trials, the largest brook trout remained at the middle and tail of each uppermost pool, patrolling the low-velocity water near the substrate. Smaller members of the two species distributed themselves relatively evenly throughout the stream-channels with no evidence of clumping by species.

In tests concerning prior residence, brook trout given residence rarely attacked newly introduced cutthroat trout (two encounters observed), and were driven from the pool within 2 hr by the cutthroat trout. When cutthroat trout held prior residence, they immediately drove all incoming brook trout from the pool or into channel corners (20 encounters observed).

Frequencies of encounters — Cutthroat trout longer than 100 mm initiated more than twice as many offensive encounters against members of their own species as did brook trout in the eight trials (395 encounters vs 189, $X^2 = 72.66$, $P < .005$). Cutthroat trout initiated nearly a third more offensive interspecific encounters than did brook trout (243 vs. 189, $X^2 = 6.76$, $P = .008$).

Cutthroat trout directed almost two-thirds of their total offensive activity toward members of their own species (395 intraspecific encounters, 243 interspecific). Brook trout divided their aggressive activity equally between cutthroat trout and other brook trout (189 encounters toward each). But since each channel contained five trout of each species, an individual could interact intraspecifically with four, and interspecifically with five. If encounters occurred at random, four-ninths of all behavior should have been intraspecific and five-ninths interspecific. Therefore both species devoted more energy to intraspecific activity than expected ($X^2 = 5.53$, $P = .013$ for brook trout, and $X^2 = 83.10$, $P < .005$ for cutthroat trout). Lateral and frontal threats, nips, and nips-close occurred infrequently, with little variation in frequency between species.

On an individual basis, dominance depended upon fish size (Table 2). The largest individual cutthroat and brook trout in each trial together initiated 42% of all offensive encounters, and were the recipients of 2%; for the smallest fish, 1 and 31% respectively. Only 9% of all offensive encounters occurred between brook and cutthroat trout of equal sizes, and most of these were between medium-sized fish. Cutthroat trout initiated 48 offensive acts against equal-sized opponents, while brook trout initiated 41.

TABLE 2. Percentages of offensive acts (total 1016) initiated and received by four brook and four cutthroat trout in each of five 15-mm size groups in large stream-channels, December 1969–March 1970.

Fish size range (*mm*)	Percentage initiated	Percentage received
	Brook trout	
100–115	0.0	9.4
116–130	3.0	14.0
131–145	9.4	10.2
146–160	7.5	8.0
161–175	17.4	0.9
Total	37.3 (378 acts)	42.5 (432 acts)
	Cutthroat	
100–115	0.8	21.2
116–130	10.3	15.0
131–145	13.9	13.6
146–160	12.7	6.6
161–175	25.0	1.1
Total	62.7 (638 acts)	57.5 (584 acts)
Grand total	100.0	100.0

Field Observations

The two species did not overlap in length during their first summer in the study streams. Cutthroat fry, from eggs spawned in May and June, emerged from gravel during the last week of July in both 1968 and 1969. By mid-August these fish averaged 30 mm in length. Since brook trout spawned in October and November, fry emerged earlier than cutthroat and averaged 20 mm longer in September. Brook trout maintained this mean size advantage throughout their lifetimes, but length distributions of yearling and older fish overlapped between species. I captured few trout of either species older than age-group III and longer than 160 mm.

During approximately 35 hr spent diving to gather microhabitat data, both intraspecific and interspecific aggressive encounters were occasionally observed. No variations from the behavior patterns noted in laboratory stream-channels were evident.

Habitat Utilization

In one stream inhabited sympatrically (Crystal Creek), an area of slack water created by beaver dams was occupied only by brook trout. A silt bottom and lack of current for fish to face made diving to assess microhabitat utilization impossible. Such separation of species was not evident in the pool-riffle environment of the other study stream inhabited by both species (Hoodoo Creek).

Within the portions of study sections where members of the two species overlapped in distribution, underyearling cutthroat trout occupied shallow sheltered areas along stream banks, and underyearling brook trout lived in deeper, faster water at the tails of pools. Adult cutthroat in pools usually lived at the upper ends, with the largest individuals farthest upstream. The older brook trout commonly held in slower waters near overhead cover at the sides and tails of the pools. No interspecific difference in habitat utilization was evident in riffles.

Microhabitat — Analysis of habitats utilized by 41 brook and 59 cutthroat trout living sympatrically (Table 3) in Hoodoo and Crystal Creeks indicated that (1) younger fish occupied shallower water than did older fish, (2) underyearling cutthroat trout occupied shallower water than did underyearling brook

TABLE 3. Average water depths, water velocities, and distances from overhead cover measured at the focal points, or centers of activity of the fish, and maximum water velocities within 0.6 m (within 0.3 m for underyearlings) of the focal points, and analyses of variance for trout in study streams, August 1968 and August 1969.

Source of variation	Age	No. fish	Water depth (m)	F	Velocity at focal point (cm/sec)	F	Maximum velocity (cm/sec)	F	Distance from cover (m)	F
					Sympatry					
					Brook trout					
	0	14	0.41		9.0		11.4		0.12	
	I	11	0.45		8.7		23.8		0.31	
	II	10	0.45		9.6		24.1		0.21	
	III+	6	0.57		7.6		12.7		0.41	
					Cutthroat trout					
	0	8	0.26		10.7		15.6		0.12	
	I	19	0.45		10.3		17.8		0.41	
	II	24	0.52		10.2		16.6		0.35	
	III+	8	0.44		10.3		29.3		0.80	
Species				3.264[a]		6.408[b]		0.151		1.599
Age				6.453[c]		0.371		1.007		3.111[b]
Species × age				3.311[b]		0.432		1.782		0.582
					Allopatry					
					Brook trout					
	0	17	0.42		8.7		16.9		0.23	
	I	20	0.66		8.8		15.7		0.44	
	II	9	0.60		10.9		25.7		0.59	
	III+	6	0.70		8.4		20.8		0.24	
					Cutthroat trout					
	0	8	0.30		7.8		11.2		0.14	
	I	18	0.46		12.4		22.2		0.58	
	II	20	0.48		11.9		22.0		0.52	
	III+	8	0.49		13.7		22.1		0.79	

[a] $P < .10$.
[b] $P < .05$.
[c] $P < .01$.

trout, (3) cutthroat trout of all ages faced greater velocities than did brook trout, (4) younger fish of both species lived closer to cover than did older fish, and (5) the oldest cutthroat lived twice as far from cover as did the oldest brook trout. Depth occupied by each species was related to age for all age-groups ($P < .01$), but species differences seemed to result from the size discrepancy between underyearlings of the two species. Underyearling cutthroat segregated from brook trout with respect to water depth, since the smaller cutthroat trout held in water about two-thirds the depth occupied by brook trout. The oldest cutthroat lived in areas of only moderate depth, while the oldest brook trout held in the deepest water.

Cutthroat trout consistently faced higher water velocity ($P < .05$), averaging 10.2–10.3 cm/sec for age-group I and older cutthroat as compared with 7.6–9.6 cm/ sec for brook trout of the same age-groups. No statistically significant differences existed between species or age-groups with regard to maximum water velocity within 0.6 m (within 0.3 m for under yearlings), but cutthroat of age-group III and older lived near current twice as swift as that near which the oldest brook trout lived.

Underyearling trout of both species occupied areas closer to overhead cover than did older trout ($P <$

.05). The oldest cutthroat lived twice as far from cover as the oldest brook trout, but interspecific differences were not statistically significant for all age-groups taken together. Approximately 60% of the brook trout and 55% of the cutthroat trout lived over a gravel substrate, with the remainder distributed over silt, sand, and rock; no consistent differences were evident between age-groups or species.

Trout living allopatrically (Table 3) in Deer and Pack Creeks occupied habitats similar to those inhabited by sympatric populations, although physical differences between the streams occupied allopatrically made statistical comparison impractical. Allopatric and sympatric cutthroat trout of all age-groups occupied areas of similar water depth. Allopatric brook trout were found at greater depths than either sympatric brook trout or allopatric cutthroat trout, reflecting the presence of deeper pools in Deer Creek. Velocities at the focal points for allopatric trout corresponded very closely to those for the species living together. No meaningful trends in values of maximum velocity near the focal points were evident for any group of fish.

Allopatrically, members of both species younger than age-group III held farther from cover than they had sympatrically. The oldest brook trout lived closer to cover than they had sympatrically, while the oldest cutthroat remained farthest from cover in positions similar to those for sympatric cutthroat. Allopatric trout lived near substrate similar to that occupied sympatrically, with over half of the members of each species living over a gravel substrate.

Discussion

Aggression

No experimental evidence was found to suggest that brook trout could displace equal-sized cutthroat trout. Individuals of the two species communicated effectively, as have juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) (Kalleberg 1958), juvenile brook and rainbow trout (Newman 1956), and brown and rainbow trout (Jenkins 1969). Juvenile cutthroat trout dominated equal-sized brook trout as young brown trout dominated similar-sized Atlantic salmon (Kalleberg 1958). But earlier emergence of brook trout fry led to the staggered spacing, at any one time, of the mean lengths of brook and cutthroat trout year-classes, similar to that of Atlantic salmon and brown trout (Egglishaw 1967), juvenile steelhead trout and chinook salmon, (*Oncorhynchus tshawytscha*) (Everest MS 1969), and juvenile chinook and coho salmon, (*Oncorhynchus kisutch*) (Lister and Genoe 1970). Consequently underyearling brook trout of the size found in the study streams in late summer dominated in experiments the underyearling cutthroat trout with which they normally lived.

Yearling and older brook trout initiated 40% fewer aggressive encounters under laboratory conditions than did equal-sized cutthroat trout, and did not displace cutthroat trout that were given prior residence. Although brook trout maintained a size advantage over equal-aged cutthroat trout in the study streams that should benefit them over many encounters, it is unlikely to offset the greater amount of aggression displayed by cutthroat trout.

Differential Vulnerability to Angling

Although this study suggests that aggressive activity of brook trout plays a minor role in the decline of cutthroat trout populations, I believe that other, more subtle mechanisms are operating, especially in pool areas, as a consequence of interspecific behavioral differences. Differential vulnerability of the species to angling has been demonstrated by MacPhee (1966). In a northern Idaho stream, experimental angling captured 50% of the 138 cutthroat trout present, but only 25% of the 316 similar-sized brook trout present before all fish were killed with rotenone. I noticed a similar trend in the study streams and attribute it to behavioral differences. The largest cutthroat, which often live at the heads of pools under a blanket of turbulent water, may be relatively unaware of a fisherman's approach; but the brook trout, along the stream banks, may be more aware of the vibrations caused by an angler's footsteps. Angling effort is usually directed to the head and center of a pool, where cutthroat are more likely to be found. Also, the greater amount of aggression exhibited by cutthroat may indicate a greater tendency to strike at moving lures.

Differences in Habitat Utilization

This and other studies in northern Idaho suggest that stream gradient may influence the distribution of brook and cutthroat trout in streams inhabited sympatrically. Although cutthroat trout may live in areas of low water velocity (below about 6 cm/sec) in Idaho when not associated with brook trout (Bjornn 1957), they did not inhabit this environment in sustained sympatry with brook trout in Crystal Creek. The gradients in Crystal and Hoodoo Creeks, in which densities of brook trout have increased over the years, were less than 3%. Bachmann (MS 1958) found brook trout in portions of Crystal Creek with low stream gradient, while cutthroat trout became more abundant upstream as the gradient increased. In a tributary of the St. Joe River, Idaho, brook trout occupied the downstream portion with a gradient below 4%, while cutthroat trout increased in num-

bers upstream as the gradient increased (MacPhee 1966).

Within the portion of Crystal Creek where the species overlapped in distribution, and within the entire study area of Hoodoo Creek, interspecific social contact of underyearlings was minimized by the utilization of disparate water depths, a consequence of differing emergence dates. Interaction between individual brook and cutthroat trout of age-group III and older was likewise minimized by their utilization of habitat differing particularly in distance from overhead cover. The greatest potential for interaction lies with fish of age-groups I and II, whose habitat characteristics, apart from water velocity at the focal point, show considerable overlap.

Comparisons of allopatric and sympatric habitat utilization indicate only minor interspecific differences for all age-groups, suggesting that these differences have developed in allopatry, and not during the 15 generations in which the species have lived sympatrically.

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Parasites of Fish from Lake of the Woods, Ontario[1]

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DECHTIAR, A. O. 1972. Parasites of fish from Lake of the Woods, Ontario. J. Fish. Res. Bd. Canada 29: 275–283.

Results of a survey of the parasite fauna of fish from Lake of the Woods and adjacent lakes are presented. Over 600 fish representing 41 species were examined, and 170 species of parasites, mostly helminths, are recorded. Every species of fish and 97% of all fish examined carried at least one parasite. No parasites considered hazardous to human health were found. A number of parasites, reported elsewhere as contributors to fish mortalities, are recorded.

DECHTIAR, A. O. 1972. Parasites of fish from Lake of the Woods, Ontario. J. Fish. Res. Bd. Canada 29: 275–283.

L'auteur fait connaître les résultats d'un recensement de la faune parasitaire des poissons du lac des Bois et des lacs avoisinants. Il a examiné plus de 600 poissons répartis en 41 espèces et a trouvé 170 espèces de parasites, des helminthes pour la plupart. Toutes les espèces de poissons et 97 pour cent des individus examinés portaient au moins un parasite. Aucun parasite nuisible à l'homme n'a été trouvé. L'auteur énumère un certain nombre de parasites signalés ailleurs comme responsables de la mortalité des poissons.

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AN extensive survey of the parasite fauna of fish in Ontario was initiated in 1960. As part of this survey, intensive fish sampling was undertaken in Lake of the Woods and in some adjacent lakes of northwestern Ontario during 1963–66. Climate and glacial history of this area distinguish it from other parts of northern Ontario. These differences are reflected in the fish fauna (Radforth 1944), which in some respects differs from the fauna in other parts of northern Ontario, and it was reasonable to expect the parasite fauna of the area to be somewhat specific.

Virtually no earlier literature is available concerning fish parasites in this area. Fischthal (1952, 1953) reported his examinations of fish from lakes and streams in northwest Wisconsin, and both Hoffmann (1941) and Carlander (1943) made reference to the occurrence of *Triaenophorus robustus* in lake herring, *Leucichthys artedii* (Lesueur), and tullibee, *Coregonus nipigon* (Koelz), from Lake of the Woods. Bangham (1946) reported 82 parasite species for fish from northern Wisconsin waters.

Materials and Methods

Fish specimens were collected from Lake of the Woods and adjacent lakes using gillnets, poundnets, and minnow seines. Some fishing was directed specifically at obtaining specimens for this study; however, most were selected from catches by gear fished for other purposes. Specimens of lake herring, for example, were selected so that a range of sizes was available for examination. No such selection was possible for less abundant or less available species. Most of the specimens were taken either in early spring or in the fall, but a few were taken throughout the open water period. Most of the fish were examined as fresh material. A small number, representatives of the less available species, were frozen or preserved in formalin. Each fish was subjected to a thorough examination. All parasites found during autopsy were preserved in 5% formalin, with the exception of crustaceans, molluscs, and round worms which were fixed and stored in glycerin alcohol. Most monogeneans and nematodes were later mounted, unstained, in glycerin jelly. Digeneans, acanthocephalans, and tapeworms were stained with Mayer's carmine, borax carmine, or Gomoris trichrome, cleared in beachwood creosote, and mounted in Piccolyte.

Common parasites were identified alive. All parasites from this survey have been retained in the author's collection at the Research Branch, Department of Lands and Forests, Maple, Ont.

Results

Each species of fish examined carried parasites. Of the fish examined, 96.8% (601) were infected with at least one species of parasite. A total of 170 parasite species were identified and recorded. Some other parasites were identified only as to genus, and

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are thought to represent new species, pending further investigation. The most abundant parasites were digeneans, 41 species, and monogeneans, 32 species. The Cestoda were represented by 9 species, Nematoda by 16 species, Crustacea by 13 species, Protozoa by 19 species, Acanthocephala by 13 species, and Hirudinea by 4 species. One species of Mollusca, a larval form, and one each of virus and fungus infections were recorded.

The results of the study are presented in detail below. Scientific and common names of fish are arranged according to Bailey et al. (1970). The parasites found in each host species are arranged according to systematic group. For each host species, the total number of specimens examined and the number infected is given. A number follows each parasite identified, indicating the number of host specimens in which the parasite was found. The letters L, M, and H following the numbers have reference to "Light" (1–10 parasites per host), "Medium" (11–50 parasites per host), and "Heavy" (over 50 parasites per host). Unless otherwise indicated by asterisks, all parasites listed are present in the adult stage. A single asterisk (*) preceding the name indicates occurrence as an 'immature' form, and a double asterisk (**) indicates occurrence as the larval form of the parasite. The principal site where the parasite was found in the host is given in each case.

Acipenser fulvescens Rafinesque — Lake sturgeon
(Examined, 1; infected, 1)
- ****Diplostomulum** sp., 1, L, eye
- *Diclybothrium armatum*, 1, M, gills
- *Crepidostomum lintoni*, 1, M, intestine

Salvelinus namaycush (Walbaum) — Lake trout
(Examined, 7; infected, 7)
- *Eubothrium salvelini*, 7, M, intestine
- *Cystidicola cristivomeri*, 7, M, air bladder
- ****Diplostomulum** sp., 4, L, eye
- ****Triaenophorus crassus**, 2, M, muscle
- *Proteocephalus parallacticus*, 4, M, intestine
- *Salmincola siscowet*, 4, M, fins
- *Metechinorhynchus salmonis*,[2] 6, M, intestine

Coregonus clupeaformis (Mitchill) — Lake whitefish
(Examined, 15; infected, 15)
- ****Diplostomulum** sp., 2, L, eye
- *Tetracotyle intermedia*, 12, L, heart, mesenteries
- *Discocotyle sagittata*[3], 3, M, gills
- *Phyllodistomum coregoni*, 9, M, ureters
- *Cyathocephalus truncatus*, 15, M, intestine
- ****Diphyllobothrium** sp., 5, L, cysts on stomach, pyloric caecum
- *Proteocephalus exiguus*, 2, L, intestine
- *Proteocephalus laruei*, 4, M, intestine
- ****Triaenophorus crassus**, 8, L, muscle
- *Metechinorhynchus lateralis*[4], 3, L, intestine
- *Metechinorhynchus salmonis*, 9, M, intestine
- *Neoechinorhynchus tumidum*, 1, L, intestine
- *Cystidicola stigmatura*, 7, L, air bladder
- *Achtheres corpulentus*, 1, L, gill arches

Coregonus artedii Lesueur — Lake herring
(Examined, 52; infected, 50)
- *Henneguya* sp., 2, M, gills
- *Discocotyle sagittata*, 22, L, gills
- ****Diplostomulum** sp., 9, L, eye
- ****Tetracotyle intermedia**, 5, L, heart, mesenteries
- *Phyllodistomum* sp., 9, L, ureters
- *Cyathocephalus truncatus*, 10, M, intestine
- ****Diphyllobothrium** sp., 12, L, cysts on stomach, pyloric caecum
- *Proteocephalus exiguus*, 18, L, intestine
- *Proteocephalus laruei*, 3, M, intestine
- ****Triaenophorus crassus**, 17, L, muscle
- *Metechinorhynchus salmonis*, 15, L, intestine
- *Neoechinorhynchus tumidum*, 7, M, intestine
- *Cystidicola stigmatura*, 8, L, air bladder
- *Spinitectus gracilis*, 4, L, intestine
- *Argulus canadensis*, 12, M, surface of the body
- *Ergasilus* sp., 3, L, gills

It is considered likely that further investigation will show the *Phyllodistomum* sp. from the urinary bladders and ureters to be a new species. *Cyathocephalus truncatus* was first reported in lake herring (Dechtiar and Loftus 1965) from Lake Huron. The occurrence here constitutes the second record.

Esox lucius Linnaeus — Northern pike
(Examined, 23; infected, 23)
- *Azygia longa*, 2, L, intestine, stomach
- *Azygia angusticauda*, 6, L, intestine, stomach
- ****Clinostomum marginatum**[5], 3, L, muscle, mesenteries
- ****Diplostomulum** sp., 7, L, eye
- ****Uvulifer ambloplitis**, 2, L, skin
- ****Tetracotyle** sp., 4, L, mesenteries
- *Tetraonchus monenteron*, 16, H, gills
- ****Posthodiplostomum minimum**, 2, L, liver, mesenteries
- *Proteocephalus pinguis*, 20, L, intestine
- *Triaenophorus nodulosus*, 11, M, intestine
- *Triaenophorus crassus*, 16, M, intestine
- *Leptorhynchoides thecatus*, 4, L, intestine
- *Metechinorhynchus salmonis*, 9, L, intestine
- *Neoechinorhynchus tenellum*, 5, L, intestine
- *Contracaecum brachyurum*, 22, M, intestine
- *Illinobdella* sp., 4, L, fins

[2]According to Petrochenko (1956) and Golvan (1969).
[3]According to Price and McMahon (1967).
[4]According to Golvan (1969).
[5]*Clinostomum marginatum* (Rudolphi 1819) is a synonym of *C. complanatum* (Rudolphi 1814), but the name *C. marginatum* has been used in North America.

In addition, immature forms of *Proteocephalus pinguis* were found in 20 hosts, of *Triaenophorus nodulosus* in seven hosts, and of *Contracaecum brachyurum* in seven hosts.

Esox masquinongy Mitchill — Muskellunge
(Examined, 2; infected, 2)
Henneguya acuta, 2, L, gills
Azygia angusticauda, 2, L, intestine
Triaenophorus nodulosus, 2, L, intestine
Triaenophorus crassus, 1, L, intestine
Leptorhynchoides thecatus, 2, L, intestine
Metechinorhynchus salmonis, 2, L, intestine
Neoechinorhynchus tenellus, 2, L, intestine
Contracaecum brachyurum, 2, L, intestine

Immature as well as adult specimens of *Azygia angusticauda* and *Contracaecum brachyurum* were found.

Umbra limi (Kirtland) — Central mudminnow
(Examined, 2; Infected, 2)
***Diplostomulum* sp., 2, L, eye
***Leptorhynchoides thecatus*, 2, L, intestine

Carpiodes cyprinus (Lesueur) — Quillback
(Examined, 5; infected, 5)
Myxosoma rotundum, 2, H, gills
Anonchohaptor anomalum, 1, L, gills, fins
Triganodistomum attenuatum, 3, L, intestine
Glaridacris confusus, 2, L, intestine
**Proteocephalus* sp., 2, L, intestine
Pomphorhynchus bulbocolli, 2, L, intestine

The above apparently constitutes a new host record for *Anonchohaptor anomalum*.

Catostomus catostomus (Forster) — Longnose sucker
(Examined, 1; infected, 1)
Phyllodistomum sp., 1, L, ureters
Tetracotyle communis, 1, M, mesenteries
Ergasilus caeruleus, 1, M, gills

Catostomus commersoni (Lacépède) — White sucker
(Examined, 51; infected, 51)
Chloromyxum catostomi, 5, M, gall bladder
Ichthyophthirius multifiliis, 5, M, fins, skin
Myxosoma catostomi, 4, L, muscle
Myxosoma bibullatum, 6, L, gills
Acolpenteron catostomi, 13, M, ureters
Allocreadium lobatum, 2, L, intestine
Anonchohaptor anomalum, 4, L, gills, fins
Crepidostomum cooperi, 6, L, intestine
***Diplostomulum flexicaudum*, 12, L, eye
Gyrodactylus spathulatus, 4, L, gills, fins,
Pseudomurraytrema copulatum, 7, M, gills
***Neascus* sp., 4, L, connective tissue
Octomacrum lanceatum, 6, L, gills
Pellucidhaptor nasalis, 6, L, nasal cavities
Plagioporus sinitsini, 3, L, intestine
Phyllodistomum lysteri, 14, L, ureters
***Tetracotyle communis*, 4, L, mesenteries
Glaridacris catostomi, 7, L, intestine
Glaridacris intermedius, 3, L, intestine
Hunterella nodulosa, 5, L, intestine
***Ligula intestinalis*, 12, L, body cavities
***Triaenophorus nodulosus*, 7, L, liver
Leptorhynchoides thecatus, 7, L, intestine
Neoechinorhynchus crassus, 7, L, intestine
Neoechinorhynchus cristatus, 8, L, intestine
Neoechinorhynchus strigosus, 2, L, intestine
Octospinifer macilentus, 2, L, intestine
Pomphorhynchus bulbocolli, 16, M, intestine
**Camallanus oxycephalus*, 4, L, intestine
***Contracaecum* sp., 4, L, liver, mesenteries
***Spiroxys* sp., 4, L, mesenteries
Argulus catostomi, 2, L, fins
Ergasilus caeruleus, 8, L, gills
***Glochidia*, 5, L, gills, fins
Actinobdella triannulata, 10, L, gill cover (internal surface)

Moxostoma anisurum (Rafinesque) — Silver redhorse
(Examined, 6; infected, 6)
Myxobolus sp., 6, L, gills
Anonchohaptor anomalum, 6, L, gills, fins
***Diplostomulum flexicaudum*, 4, L, eye
Gyrodactylus spathulatus, 6, L, fins, gills
Neascus sp., 1, L, skin
Pseudomurraytrema copulatum, 6, L, gills
Pseudomurraytrema sp., 6, L, gills
Sanguinicola sp., 4, L, blood
Triganodistomum attenuatum, 1, L, intestine
Biacetabulum infrequens, 2, L, intestine
***Triaenophorus nodulosus*, 3, L, liver
Leptorhynchoides thecatus, 1, L, intestine
***Contracaecum brachyurum*, 1, L, liver, mesenteries
Spinitectus gracilis, 1, L, intestine
Ergasilus caeruleus, 1, L, gills

Further study is thought likely to show the *Sanguinicola* sp. to be a new species.

Moxostoma erythrurum (Rafinesque) — Golden redhorse
(Examined, 4; infected, 4)
Myxobolus sp., 3, M, gills
Anonchohaptor anomalum, 4, L, gills, fins
Dactylogyrus urus, 4, L, gills
Pseudomurraytrema sp., 4, L, gills
Ergasilus caeruleus, 2, L, gills
Ergasilus sp., 2, L, gills

Chrosomus neogaeus (Cope) — Finescale dace
(Examined, 11; infected, 9)
Myxobolus conspicuus, 9, L, skin
Cleidodiscus brachus, 9, L, gills
***Neascus* sp., 1, L, connective tissue
Octomacrum semotili, 9, L, gills
***Posthodiplostomum minimum*, 1, L, liver, mesenteries

****Tetracotyle communis*, 1, L, mesenteries
***Proteocephalus* sp., 1, L, intestine

Couesius plumbeus (Agassiz) — Lake chub
(Examined, 5; infected, 5)
Dactylogyrus mylocheilus, 2, L, gills
****Diplostomulum* sp., 3, L, eye
****Neascus* sp., 3, L, skin
Octomacrum sp., 2, L, gills

Notemigonus crysoleucas (Mitchill) — Golden shiner
(Examined, 2; infected, 2)
Dactylogyrus parvicirrus, 2, L, gills
****Diplostomulum* sp., 2, L, eye
Octomacrum microconfibula, 2, L, gills
****Posthodiplostomum minimum*, 1, L, liver, mesenteries

Notropis anogenus (Forbes) — Pugnose shiner
(Examined, 8; infected, 8)
****Diplostomulum* sp., 2, L, eye
Gyrodactylus sp., 4, M, gills
****Neascus* sp., 2, L, skin
Rhabdochona cascadilla, 1, L, intestine
Leptorhynchoides thecatus, 1, L, intestine

Notropis atherinoides Rafinesque — Emerald shiner
(Examined, 9; infected, 8)
****Diplostomulum* sp., 2, L, eye
***Bothriocephalus cuspidatus*, 2, L, intestine
***Proteocephalus pearsei*, 2, L, intestine
***Contracaecum brachyurum*, 2, M, intestine
***Neoechinorhynchus* sp., 2, M, intestine

Notropis hudsonius (Clinton) — Spottail shiner
(Examined, 25; infected, 24)
Myxosoma grandis, 6, M, liver
****Clinostomum marginatum*, 1, L, muscle
Dactylogyrus sp., 4, L, gills
****Diplostomulum* sp., 4, L, eye
****Tetracotyle* sp., 5, L, mesenteries
****Neascus* sp., 13, L, skin
****Posthodiplostomum minimum*, 4, L, liver, mesenteries
Neoechinorhynchus sp., 3, L, intestine
****Contracaecum* sp., 4, L, liver
Rhabdochona cascadilla, 2, L, intestine
****Ligula intestinalis*, 4, L, body cavity
Argulus canadensis, 1, L, fins, body
Ergasilus sp., 3, L, gills

Notropis heterolepis (Eigenmann and Eigenmann) — Blacknose shiner
(Examined, 3; infected, 3)
****Diplostomulum* sp., 3, L, eye
****Posthodiplostomum minimum*, 3, H, liver

Pimephales notatus (Rafinesque) — Bluntnose minnow
(Examined, 20; infected, 19)
Nosema pimephales, 3, H, internal organs, muscle
****Clinostomum marginatum*, 2, L, muscle
Dactylogyrus bifurcatus, 9, L, gills
****Diplostomulum* sp., 5, L, eye
****Posthodiplostomum minimum*, 5, L, liver
Sanguinicola sp., 6, L, blood
****Tetracotyle* sp., 11, L, mesenteries
****Ligula intestinalis*, 4, L, body cavity
Neoechinorhynchus sp., 6, L, intestine

It is thought that the *Sanguinicola* sp. will prove to be a new species.

Pimephales promelas (Rafinesque) — Fathead minnow
(Examined, 6; infected, 6)
Nosema pimephales, 2, H, muscle
Allocreadium lobatum, 1, L, intestine
Dactylogyrus sp., 6, H, gills
****Diplostomulum* sp., 2, M, eye
****Neascus* sp., 2, L, skin
****Posthodiplostomum minimum*, 3, L, liver
Sanguinicola sp., 20, L, blood
***Biacetabulum* sp., 1, L, intestine

Again, the *Sanguinicola* sp. is considered likely to be a new species.

Rhinichthys atratulus (Hermann) — Blacknose dace
(Examined, 1; infected, 1)
****Postodiplostomum minimum*, 1, L, liver
Rhabdochona cascadilla, 1, L, intestine
***Leptorhynchoides thecatus*, 1, L, intestine

Rhinichthys cataractae (Valenciennes) — Longnose dace
(Examined, 2; infected, 2)
Myxobolus sp., 2, L, gills
Allocredium lobatum, 2, L, intestine
Dactylogyrus banghami, 1, L, gills
****Diplostomulum* sp., 1, L, eye
Diplostomulum scheuringi, 2, L, eye (vitreous chamber)
****Neascus* sp., 2, L, skin
****Posthodiplostomum minimum*, 2, H, liver
****Tetracotyle* sp., 1, L, mesenteries

Semotilus margarita (Cope) — Pearl dace
(Examined, 5; infected, 5)
Myxobolus sp., 2, M, gills
Octomacrum semotili, 3, L, gills

Ictalurus nebulosus (Lesueur) — Brown bullhead
(Examined, 20; infected, 20)
Myxobolus sp., 4, M, gills
Trichophrya sp., 4, M, gills
Allocreadium ictaluri, 1, L, intestine
Alloglosidium geminus, 2, L, intestine
***Azygia angusticauda*, 5, L, intestine
Cleidodiscus pricei, 20, M, gills
****Clinostomum marginatum*, 6, L, muscle
Crepidostomum ictaluri, 5, L, intestine
****Diplostomulum* sp., 6, L, eye
Phyllodistomum staffordi, 5, L, ureters
****Tetracotyle* sp., 11, L, mesenteries, kidney
***Bothriocephalus cuspidatus*, 2, L, intestine
Corallobothrium fimbriatum, 13, L, intestine
****Proteocephalus ambloplitis*, 14, L, mesenteries
Leptorhynchoides thecatus, 17, L, intestine

Metechinorhynchus salmonis, 2, L, intestine
Pomphorhynchus bulbocolli, 3, L, intestine
****Contracaecum* sp., 6, L, mesenteries, liver
Spinitectus carolini, 4, L, intestine
Ergasilus versicolor, 6, L, gills
****Glochidia*, 7, L, gills, fins
Saprolegnia sp., 3, L, fins, skin

In addition to the adult specimens of *Corallobothrium fimbriatum*, immature specimens were found in 13 bullheads.

Noturus gyrinus (Mitchill) — Tadpole madtom
(Examined, 11; infected, 10)
Myxobolus sp., 2, M, gills
Crepidostomum cornutum, 2, L, intestine
Gyrodactylus sp., 3, M, gills
**Corallobothrium fimbriatum*, 10, L, intestine
Alloglossidium corti, 3, L, intestine
**Leptorhynchoides thecatus*, 6, L, intestine
Pomphorhynchus bulbocolli, 3, L, intestine

Lota lota (Linnaeus) — Burbot
(Examined, 17; infected, 17)
Myxobolus sp., 9, H, gills
Trichodina sp., 4, H, urine bladder
Azygia angusticauda, 4, L, intestine
****Diplostomulum* sp., 7, L, eye
****Tetracotyle* sp., 9, L, mesenteries
Eubothrium rugosum, 14, H, intestine
****Triaenophorus nodulosus*, 2, L, liver
Leptorhynchoides thecatus, 7, L, intestine
Metechinorhynchus salmonis, 12, L, intestine
Pomphorhynchus bulbocolli, 3, L, intestine
**Camallanus oxycephalus*, 2, L, intestine
Contracaecum brachyurum, 9, M, intestine
Dichelyne cotylophora, 3, L, intestine
Capillaria bakeri, 3, L, intestine
Rhabdochona cascadilla, 4, L, intestine
Spinitectus gracilis, 2, L, intestine
Ergasilus osburni, 6, L, gills
Piscicola punctata, 3, L, fins
****Glochidia*, 12, L, gills

Culaea inconstans (Kirtland) — Brook stickleback
(Examined, 17; infected, 17)
Bunoderina eucaliae, 5, L, intestine
Dactylogyrus eucalius, 6, L, gills
****Diplostomulum baeri eucaliae*, 4, M, brain
Gyrodactylus eucaliae, 4, L, gills
****Neascus* sp., 4, L, skin
****Tetracotyle* sp., 3, L, mesenteries
****Proteocephalus ambloplitis*, 3, L, liver
****Agamonema* sp., 3, L, mesenteries
**Camallanus oxycephalus*, 4, L, intestine
Leptorhynchoides thecatus, 3, L, intestine
Neoechinorhynchus rutili, 2, L, intestine

Pungitius pungitius (Linnaeus) — Ninespine stickleback
(Examined, 4; infected, 4)
Myxobolus sp., 1, H, gills
Bunoderina eucaliae, 1, L, intestine
****Tetracotyle* sp., 4, L, mesenteries
Proteocephalus sp., 2, L, intestine
Leptorhynchoides thecatus, 3, L, intestine
****Glochidia*, 3, L, fins

Percopsis omiscomaycus (Walbaum) — Trout-perch
(Examined, 13; infected, 13)
Myxosoma procerum, 3, H, gills
Trichodina sp., 3, H, gills
Crepidostomum isostomum, 4, L, intestine
****Diplostomulum* sp., 12, L, eye
Gyrodactylus sp., 10, M, gills
****Tetracotyle communis*, 13, M, liver, mesenteries
Bothriocephalus formosus, 3, L, intestine
****Triaenophorus stizostedionis*, 2, L, liver
**Contracaecum brachyurum*, 2, L, intestine
Spinitectus gracilis, 2, L, intestine
Argulus versicolor, 2, L, fins

In addition to the immature *Contracaecum brachyurum*, adults were also found in 3 trout-perch.

Ambloplites rupestris (Rafinesque) — Rock bass
(Examined, 20; infected, 18)
Myxobolus sp., 5, M, intestine wall
Gyrodactylus sp., 13, M, gills
**Azygia angusticauda*, 6, L, intestine
Crepidostomum cornutum, 7, M, intestine
****Clinostomum marginatum*, 8, M, muscle
Cryptogonimus chilli, 8, M, intestine
****Diplostomulum* sp., 7, L, eye
****Tetracotyle* sp., 5, M, mesenteries
Bothriocephalus claviceps, 6, L, intestine
****Proteocephalus ambloplitis*, 4, L, liver, mesenteries
Leptorhynchoides thecatus, 10, L, intestine
Neoechinorhynchus cylindratus, 4, L, intestine
Capillaria catenata, 2, L, intestine
****Contracaecum brachyurum*, 4, M, liver
Rhabdochona cascadilla, 5, L, intestine
Spinitectus carolini, 3, L, intestine
Achtheres micropteri, 1, L, gill arches
Ergasilus caeruleus, 7, L, gills
Ergasilus centrarchidarum, 7, L, gills

Lepomis gibbosus (Linnaeus) — Pumpkinseed
(Examined, 16; infected, 16)
Chloromyxum gibbosum, 3, L, gall bladder
Myxobolus sp., 3, L, connective tissue
Gyrodactylus macrochiri, 2, L, gills
**Azygia angusticauda*, 3, L, intestine
****Clinostomum marginatum*, 6, L, muscle
**Crepidostomum cooperi*, 6, L, intestine
****Diplostomulum scheuringi*, 8, L, eye
****Diplostomulum* sp., 8, L, eye
****Neascus* sp., 4, L, skin
****Posthodiplostomum minimum*, 6, H, liver
****Tetracotyle* sp., 12, L, mesenteries
**Bothriocephalus claviceps*, 2, L, intestine
****Proteocephalus ambloplitis*, 12, H, liver, mesenteries
****Triaenophorus nodulosus*, 4, L, liver
****Contracaecum* sp., 4, L, liver
Leptorhynchoides thecatus, 4, L, intestine

Immature as well as adult *Leptorhynchoides thecatus* were recorded.

Micropterus dolomieui Lacépède — Smallmouth bass
(Examined, 37; infected, 37)
Myxobolus osburni, 6, L, mesenteries
Actinocleidus fusiformis, 27, H, gills
Cleidodiscus banghami, 27, H, gills
Azygia angusticauda, 2, L, intestine
Caecincola parvulus, 3, L, intestine
Crepidostomum cooperi, 12, L, intestine
****Clinostomum marginatum*, 10, M, muscle
****Diplostomulum* sp., 12, L, eye
Microphalus opacus, 6, L, intestine
Neochasmus umbelus, 2, L, intestine
Tetracotyle sp., 7, L, mesenteries
****Uvulifer ambloplitis*, 8, L, skin, fins
Proteocephalus ambloplitis, 24, L, intestine
Proteocephalus fluviatilis, 6, L, intestine
Leptorhynchoides thecatus, 30, L–H, intestine
Neoechinorhynchus cylindratus, 32, L–M, intestine
****Agamonema* sp., 4, L, liver, mesenteries
***Camallanus oxycephalis*, 8, L, intestine
***Contracaecum* sp., 10, L, intestine
Philometra sp., 1, L, body cavity
Ergasilus caeruleus, 8, L, gills
Ergasilus centrarchidarum, 12, L, gills

Infection of smallmouth bass by *Proteocephalus ambloplitis* was considered severe. In addition to the adult parasites in 24 fish, 30 fish contained the larval stage. Adhesions in the viscera were severe. *Leptorhynchoides thecatus* was present in the immature stage in 4 fish, in addition to the adults.

Pomoxis nigromaculatus (Lesueur) — Black crappie
(Examined, 40; infected, 36)
Myxobolus intestinalis, 4, L, intestine wall
Trichodina sp., 5, L, gills
Cleidodiscus capax, 8, L, gills
****Diplostomulum scheuringi*, 3, L, eye
****Diplostomulum*, sp., 2, L, eye
****Neascus* sp., 4, L, skin
****Posthodiplostomum minimum*, 1, L, liver
****Tetracotyle* sp., 3, L, mesenteries
****Proteocephalus ambloplitis*, 8, L, liver
***Proteocephalus pearsei*, 3, L, intestine
***Bothriocephalus* sp., 3, L, intestine
Leptorhynchoides thecatus, 7, L, intestine
Spinitectus gracilis, 2, L, intestine
Ergasilus caeruleus, 8, L, gills

Immature specimens of *Leptorhynchoides thecatus* were also present in 3 black crappies.

Perca flavescens (Mitchill) — Yellow perch
(Examined, 67; infected, 65)
Ichthyophthirius multifiliis, 5, L, fins, operculum, gills
Myxobolus percae, 6, H, eye
Trichodina sp., 9, H, ureters
Cleidodiscus adspectus[6], 27, M, gills
****Apophalus itascensis*, 23, M, muscle
Bunodera sacculata, 3, M, intestine
Centrovarium lobotes, 2, M, intestine
****Clinostomum marginatum*, 4, L, muscle
****Crassiphiala bulboglossa*, 9, M, skin
****Diplostomulum scheuringi*, 17, L, eye
****Diplostomulum* sp., 25, L, brain
Phyllodistomum superbum, 18, M, ureters
****Tetracotyle* sp., 15, L, mesenteries
***Bothriocephalus cuspidatus*, 6, L, intestine
Cyathocephalus truncatus, 6, L, pyloric caecum
****Proteocephalus ambloplitis*, 16, L, liver, mesenteries
Proteocephalus pearsei, 12, L, intestine
****Triaenophorus nodulosus*, 12, L, liver
Leptorhynchoides thecatus, 18, L, intestine
***Camallanus oxycephalus*, 8, L, intestine
****Contracaecum* sp., 6, L, liver, mesenteries
Dichelyne cotylophora, 9, L, intestine
****Eustrongylides* sp., 1, L, cysts attached to visceral organs
Philometra cylindracea, 5, M, body cavity
Philometra sp., 1, L, body cavity
Spinitectus gracilis, 7, L, intestine
Argulus canadensis, 6, L, fins
Ergasilus caeruleus, 21, L, gills
****Glochidia, 10, L, gills
Illinobdella sp., 5, L, fins
Saprolegnia sp., 4, L, fins, skin

Immature specimens of *Proteocephalus pearsei* were found in 10 hosts, in addition to the adults. In all, yellow perch carried 31 species of parasites.

Stizostedion canadense (Smith) — Sauger
(Examined, 18; infected, 18)
Cleidodiscus aculeatus, 15, L–M, gills
Centrovarium lobotes, 8, L, intestine
****Clinostomum marginatum*, 6, L, muscle
Bucephalus pusillus, 4, L, intestine
****Diplostomulum* sp., 6, L, eye
****Neascus* sp., 8, L, skin
Phyllodistomum superbum, 10, L, ureters
****Tetracotyle communis*, 10, L, mesenteries
Bothriocephalus cuspidatus, 15, L–M, intestine
****Proteocephalus ambloplitis*, 8, L, mesenteries
Proteocephalus stizostethi, 6, L–M, intestine
****Triaenophorus nodulosus*, 4, L, liver, mesenteries
Metechinorhynchus salmonis, 8, L, intestine
Neoechinorhynchus tenellus, 15, L–M, intestine
***Camallanus oxycephalus*, 2, L, intestine
Contracaecum brachyurum, 6, L, intestine
****Eustrongylides* sp., 1, L, cysts in body cavity
Argulus appendiculosus, 5, L, fins
Ergasilus caeruleus, 16, L–H, gills
Illinobdella moorei, 12, L, fins
****Glochidia, 12, L, gills

[6]According to Price and Mura (1969), genus *Urocleidus* is a synonym of *Cleidodiscus*.

In addition to the adults, immature specimens of *Bothriocephalus cuspidatus* were found, and also larval *Contracaecum brachyurum* specimens in one sauger.

Stizostedion v. vitreum (Mitchill) — Walleye
(Examined, 29; infected, 28)
Lymphocystis, 6, L–H, skin
Azygia angusticauda, 4, L, intestine
Bunodera sacculata, 6, L, intestine
****Clinostomum marginatum*, 4, L, muscle
****Diplostomulum scheuringi*, 4, L, eye
****Diplostomulum* sp., 5, L, eye
****Tetracotyle communis*, 14, L, mesenteries
Phyllodistomum superbum, 10, L, ureters
Cleidodiscus aculeatus, 16, L–H, gills
Bothriocephalus cuspidatus, 29, L–H, intestine
****Proteocephalus ambloplitis*, 11, L, mesenteries, liver
Proteocephalus stizostethi, 8, L, intestine
Triaenophorus stizostedionis, 6, L, intestine
Metechinorhynchus salmonis, 12, L, intestine
Neoechinorhynchus tenellus, 23, L, intestine
Contracaecum brachyurum, 16, L, intestine
****Eustrongylides* sp., 2, L, cyst in muscles
Argulus canadensis, 7, L, fins
Argulus versicolor, 5, L, fins
Ergasilus caeruleus, 29, L–H gills
Ergasilus centrarchidarum, 11, L–H, gills
**Glochidia, 6, L, gills
Illinobdella moorei, 18, L, fins

In addition, immature forms of three parasites, *Bothriocephalus cuspidatus*, *Proteocephalus stizostethi*, and *Triaenophorus stizostedionis* were recorded from 24, 11, and 8 walleyes respectively. In all, 23 parasite species were recorded from walleye.

Etheostoma exile (Girard) — Iowa darter
(Examined, 16; infected, 15)
Epistylis sp., 2, L, gills
Myxobolus sp., 3, M, wall of intestine
Gyrodactylus sp., 7, L, fins
****Apophalus itascensis*, 4, M, muscle
Azygia angusticauda, 2, L, intestine
****Diplostomulum* sp., 6, L, eye
****Neascus* sp., 3, L, skin
****Tetracotyle* sp., 6, L, mesenteries
Bothriocephalus formosus, 3, L, intestine
****Leptorhynchoides thecatus*, 7, L–M, cysts attached to mesenteries
***Camallanus oxycephalus*, 3, L, intestine
****Contracaecum* sp., 3, L, mesenteries
Rhabdochona cascadilla, 5, L–M, intestine
Argulus catostomi, 4, L, fins

Etheostoma nigrum (Rafinesque) — Johnny darter
(Examined, 24; infected, 22)
Myxobolus sp., 4, M, muscle
Gyrodactylus sp., 19, L–M, fins
****Apophalus itascensis*, 4, L, muscle
Azygia angusticauda, 3, L, intestine
****Clinostomum marginatum*, 6, L, muscle
****Diplostomulum* sp., 10, L, eye
****Tetracotyle* sp., 16, L–H, mesenteries
Leptorhynchoides thecatus, 11, L, intestine
****Contracaecum* sp., 5, L, liver, mesenteries
Rhabdochona cascadilla, 4, L, intestine
Argulus catostomi, 3, L, fins

Percina caprodes (Rafinesque) — Log perch
(Examined, 35; infected, 35)
Myxobolus sp., 4, L–M, gills
Cleidodiscus malleus, 15, L–M, gills
Trichodina sp., 6, L–M, gills
Crepidostomum isostomum, 8, L, intestine
****Diplostomulum scheuringi*, 5, L, eye
****Diplostomulum* sp., 5, L, eye
****Neascus* sp., 4, L–M, skin
****Posthodiplostomum minimum*, 5, L–M, liver
Bothriocephalus formosus, 7, L, intestine
Leptorhynchoides thecatus, 8, L–M, intestine
Pomphorhynchus bulbocolli, 2, L, intestine
***Camallanus oxycephalus*, 5, L, intestine
****Contracaecum* sp., 12, L, liver
Ergasilus caeruleus, 3, L, gills
Piscicola punctata, 10, L, fins

In addition, *Leptorhynchoides thecatus* were present as larvae in seven logperch, and immature specimens of *Camallanus oxycephalus* were found in three.

Cottus bairdi Girard — Mottled sculpin
(Examined, 10; infected, 10)
Myxobolus sp., 2, M, gills
Trichodina sp., 4, M, gills
Dactylogyrus sp., 8, L–M, gills
****Diplostomulum* sp., 8, L–M, eye
Gyrodactylus bairdi, 4, L, gills
Phyllodistomum undulans, 4, L, ureters
****Tetracotyle* sp., 12, L–M, mesenteries
****Proteocephalus ambloplitis*, 4, L, liver
***Schistocephalus solidus*, 3, L, body cavity
Metechinorhynchus salmonis, 4, L, intestine
Neoechinorhynchus rutili, 2, L, intestine
****Contracaecum* sp., 4, L, liver
***Camallanus oxycephalus*, 5, L, intestine
Rhabdochona cotti, 6, L, intestine
**Glochidia, 3, L, gills

Discussion

No major mortalities of fish populations in Lake of the Woods, attributable to the effects of parasites, have been recorded. However, this survey records the occurrence of parasites that have contributed to problems elsewhere, and that therefore merit some concern in this part of Ontario.

The protozoan *Ichthyophthirius multifiliis* was found in white suckers and in yellow perch. This parasite is reported to have caused weight loss and some

mortality among fish (Davis 1944; Elser 1955; Johnson 1961; Allison and Kelly 1963).

Microsporidea and myxosporidea were found in the gills, muscle, eyes, internal organs, and skin of a number of species. Dogiel et al (1961) and Reichenbach-Klinke and Elkan (1965) indicate that myxosporidea on gill and in muscle tissue cause extensive damage to the host.

Trematodes in the larval stage (*Clinostomum marginatum*, *Diplostomulum* sp., *Posthodiplostomum minimum* and *Tetracotyle* spp.) and the adult stage of *Sanguinicola* spp. occurred commonly. Mortalities of young fish caused by infections with these parasites have been recorded (Meyer 1958; Wales 1958; Leger 1930; Bychovskaya-Pavlovskaya and Petrushevski 1963).

The adult monogeneans *Discocotyle sagittata*, *Dactylogyrus* spp., and *Gyrodactylus* spp. are considered dangerous to fish (Mizelle 1938; Tripathi 1959; Prost 1963).

The cestodes *Cyathocephalus truncatus* (adult), and the larval stages of *Triaenophorus nodulosus*, *Triaenophorus crassus*, *Ligula intestinalis*, *Diphyllobothrium* spp., and *Proteocephalus ambloplitis* are considered to merit concern. Vik (1954, 1958) reported that *Cyathocephalus truncatus*, occurring in the adult form, can cause serious damage to its host. The larval stage of *Triaenophorus nodulosus* occurs encysted in the liver and mesenteries, and is capable of causing serious liver tissue damage. Matthey (1963) reported a perch mortality that was apparently caused by a heavy infection by this parasite. The occurrence of the larval stage of *Triaenophorus crassus* in the musculature of coregonid and salmonid (Alaska) fish, and the economic difficulties which this condition has caused, is well documented (Miller 1945, 1952; Uzmann and Hesselholt 1957). The larval stage of *Diphyllobothrium* spp. occurred in lake herring, whitefish, and lake trout. Vik (1965) considered that larvae of this genus contributed to a major decline of *Salmo trutta* and *Salvelinus alpinus* in Norway. Duguid and Sheppard (1944) recorded an epizootic among trout in Wales, and Hoffman and Dunbar (1961) reported an epizootic in a population of *Salvelinus fontinalis* caused by the plerocercoids of *Diphyllobothrium* sp.[7] Infections by the bass tapeworm, *Proteocephalus ambloplitis*, appear to be serious in Lake of the Woods fish. Adults were present in 65%, and larvae in 81%, of smallmouth bass. In addition, 38% of walleyes examined were infected, particularly in the ovaries.

Among the acanthocephalans recorded in this study, *Pomphorhynchus bulbocolli* and *Metechinorhynchus salmonis* are considered serious fish pathogens. Damage to the epithelium and proliferation of connective tissue were noted in catostomids from Lake of the Woods, a situation similar to that reported by Bullock (1963).

Crustacea were represented among the pathogens by four species of *Argulus* that were detected on five different fish species. Mortalities among yellow perch and walleyes have been attributed to the effects of *Argulus* (Schumacher 1952; Allum and Hugghins 1959).

[7]According to Woodbury (1935) final hosts are pelicans and gulls.

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The Interrelation of Biting and Filtering in the Feeding Activity of the Northern Anchovy (*Engraulis mordax*)

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O'CONNELL, C. P. 1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Bd. Canada 29: 285–293.

A previous study showed that the northern anchovy (*Engraulis mordax*) captures *Artemia* adults (3.7 mm long) by biting and *Artemia* nauplii (0.65 mm long) by filter feeding. This study shows that the ratio of biting to filtering activity in small schools varies with the relative concentration of *Artemia* adults and nauplii in the water. Activity was half biting and half filter feeding when *Artemia* adults were 2% by dry weight of the available biomass, but was entirely biting when *Artemia* adults exceeded about 7% of the biomass.

It is estimated that when feeding activity is half biting and half filtering, *Artemia* adults and nauplii would contribute equal dry weights to ingestion, and that the sum of the two would be the same as that possible if total activity had been filtering. When relative concentration of *Artemia* adults is high enough to induce total biting activity, the dry weight ingested per unit time would be double that possible by filtering alone on the nauplii present.

Ratios of large-to-small crustaceans are relatively high near the surface at night off southern California, which suggests that biting activity could often exceed 50% of total feeding activity. If the plankton does support a high percentage of biting activity, a large part of the area should usually provide the anchovy with its daily nutritional needs.

O'CONNELL, C. P. 1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Bd. Canada 29: 285–293.

Une étude antérieure a démontré que les anchois (*Engraulis mordax*) capturent les *Artemia* adultes (3.7 mm) à coups de dents et qu'elles se nourrissent par filtration de nauplii d'*Artemia* (0.65 mm). La présente étude révèle que le rapport morsure–filtration dans les bancs de taille restreinte varie en fonction de l'abondance relative des *Artemia* adultes et des nauplii dans le milieu. L'alimentation se fait moitié par morsure, moitié par filtration, quand les *Artemia* adultes constituent 2% en poids sec de la biomasse disponible, mais entièrement par morsure quand les *Artemia* adultes dépassent environ 7% de la biomasse.

Nous estimons que lorsque l'alimentation se fait moitié par morsure, moitié par filtration, les quantités d'*Artemia* adultes ingérées sont les mêmes en poids sec que celles des nauplii, et que le total des deux équivaut au total possible par filtration seulement. Lorsque la concentration en *Artemia* est suffisante pour induire une activité entièrement de morsure, le poids sec ingéré par unité de temps serait deux fois plus grand que celui possible par filtration seulement des nauplii.

La proportion des gros crustacés par rapport aux petits est relativement élevée près de la surface, la nuit, au large de la Californie méridionale. La morsure constituerait donc plus de 50% de l'activité alimentaire totale. Si, en réalité, le plancton est l'objet d'un fort pourcentage de morsure, une grande partie de la région pourrait généralement répondre aux besoins alimentaires quotidiens de l'anchois.

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LEONG and O'Connell (1969) showed that the northern anchovy (*Engraulis mordax*) captured *Artemia* nauplii by filtering, but captured the much larger *Artemia* adults individually by directed biting (particulate feeding) when each food was presented separately. Food biomass was accumulated more rapidly by biting than by filtering. They hypothesized that the anchovy could not sustain its daily food requirement by filtering alone off southern California, except in limited areas of heavy plankton concentration. Their study suggested that the role of biting activity could not be satisfactorily appraised until the response of the fish to mixed size assemblages of food organisms was better understood.

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The ability of the anchovy to capture larger but less abundant organisms by biting in addition to capturing the more numerous small organisms by filtering could be advantageous for two reasons. First, larger crustaceans with good escape responses might avoid capture by filtration. The directed nature of biting probably overcomes the escape response. Second, a greater volume of water can be searched in biting than can be strained in filtering. Either of these factors could raise the average amount of food eaten above what it would be by filtering alone.

The two modes of feeding suggest that the anchovy is a selective feeder. A number of authors have suggested on the basis of field studies that clupeoid fishes feed selectively and that food-organism size is a major determinant. Hiatt (1951), for example, showed that the nehu (*Stolephorus purpureus*) was larger and tended to have more food in its stomach in areas where large crustaceans were more available, and appeared to select these organisms. Brooks and Dodson (1965) concluded that the alewife (*Alosa pseudoharengus*) tended to select the larger crustaceans. Shen (1969) showed that zooplankters were generally more numerous than phytoplankters in the stomachs of *Engraulis japonicus*, and that the larger organisms, up to 5 mm long (Euphausiacea, Ostracoda, *Paracalanus*, and Rotifera), were commonly present in the stomachs, though only occasionally in relatively high abundance. Loukashkin (1970) showed that zooplankters were usually far more abundant than phytoplankters in the stomachs of *E. mordax*, and concluded that large copepods and euphausiids were the most important food items.

These studies imply that larger crustaceans are taken in preference to smaller organisms as their relative abundance permits. They suggest the hypothesis that ingestion rate will vary in respect to biomass concentration of plankton as the proportion of biting to filtering activity varies in some way with the relative abundance of large and small organisms in the concentration. This study attempts to describe the way in which these two kinds of feeding activity are used by small schools of anchovies in the laboratory when they are presented with different density combinations of *Artemia* adults and nauplii. The implications of these results are discussed in relation to anchovy feeding in the sea.

Procedure

Feeding trials were carried out in an arrangement of two plastic pools with connecting trough and gates (Leong and O'Connell 1969). The pools were supplied with a continuous flow of filtered sea water and each contained 3.65 m^3 of water at a depth of 0.5 m. The pools were under a 12-hr day–12-hr night cycle of illumination, but all trials were during the day. Temperature ranged from 16 to 19 C.

For each trial, water flow was turned off and 16–20 fish were diverted from a large reserve school in one pool to the trough and then admitted to a prepared food situation in the other pool. Three observers scored feeding activity for a period of 8 min, after which the fish were returned to the reserve school. All trials were preceded by at least 24 hr without feeding and samples from the reserve school always showed empty digestive tracts.

The food situation was established for each trial by placing a known number of *Artemia* adults averaging 3.7 mm long (0.5 mg dry wt) and an approximately known number of Artemia nauplii averaging 0.65 mm long (0.00145 mg dry wt) in the experimental pool and dispersing them by stirring gently with wide mesh dipnets. *Artemia* adults were precounted for all but a few high density trials, for which they were estimated by wet weight. Post-trial estimates of nauplii density were made from samples taken from the pool just before the fish were admitted.

The basic units of observation over the 8-min feeding period were 10-sec intervals marked by an audible timing device. Each of the three observers recorded the activity of a single fish as biting (B), filtering (F), or none (0) for successive intervals. The two kinds of activity, which differ by a factor of at least 10 in duration of mouth opening (Leong and O'Connell 1969), were easily distinguished. Instances of one fish displaying both kinds of activity in the same 10-sec interval were rare. Prior to each trial, each observer was assigned a different part of the school — front, middle, or rear — and chose fish in these approximate positions at the start of each interval. Observer differences will be considered in conjunction with the analysis of position differences in activity.

A pilot study indicated that the proportion of biting to filtering activity in the school might vary in relation to the relative concentration of the two sizes of *Artemia* in the water, only when *Artemia* adults were at fractions of less than about 10% of the dry weight of total food concentration. Feeding activity appeared to be directed almost entirely at larger organisms when they constituted greater fractions than this of the available food. Groups of six fish allowed to feed for 5 min averaged 56% of adult *Artemia* in dry weight of digestive tract contents, when these larger organisms were 5% or less by dry weight of the food in the water (four trials), but averaged 95% or more adults in digestive tract contents when adults were between 7 and 99% of the food in the water. The experiment was therefore limited to density combinations in which *Artemia* adults were a small fraction of the total dry weight of available food. The fractions varied from 0.4 to 11% of total dry weight, with over half of the trials having 3% or less and another one-third having between 3 and 7%. The density ranges of each food type were extended as far as practicable within this limitation.

The pilot study also suggested that a behavioral measurement would probably be a more reliable indicator of the response to the food situation existing at the start of each trial than would digestive tract

contents. Though both activities were evident in the trials that showed approximately equal dry weight fractions of the two food types in digestive tracts, and biting was distinctly dominant in the other trials, activity did appear to shift towards less biting and more filtering in the last few minutes in a few cases. Such change probably signified elimination of all or most of the larger organisms as feeding progressed.

Effect of *Artemia* Adult and Nauplii Densities on the Proportion of Biting to Filtering Activity

The response of the school to food concentrations in which *Artemia* adults were a small fraction of total dry weight at the start of the trial is described from the feeding activity occurring in the first 3 min of 46 trials. Though response was measured for 8 min, biting activity tended to be constant and maximal only during the first 3, as indicated by activity averaged for all trials (front bars in Fig. 1). Filtering activity was not maximal in the first 3 min, but rather started low and increased steadily over the feeding period. Schools exposed to nauplii alone (rear bars in Fig. 1) showed the same kind of steady increase in filtering activity.

Though interpretation of the first minute is uncertain, the response patterns in general suggest that where *Artemia* adults are present along with nauplii, biting tends to replace filtering rather than be in addition to it.

Figures 2 and 3 show the relation of biting and filtering activity in the first 3 min of feeding to the starting densities of *Artemia* adults and nauplii. Biting tended to increase with adult density and filtering tended to increase with nauplii density, but in each case the relation of response to density appeared to be lower where densities of the alternative food were higher. This suggests that the school shows a ratio of biting to filtering activity that varies with the densities of both groups of *Artemia*.

Table 1 indicates the effect of each type of food on the relative amounts of biting and filtering, which was calculated as percent biting (the ratio of 10-sec time units scored as biting to the total scored as biting and filtering in the first 3 min). The table is based on the 24 trials with *Artemia* adults between 4 and 50/m³ and *Artemia* nauplii between 100,000 and 500,000/m³. The distribution of these trials permitted separation into four equal groups representing low and high density treatments of comparable range for each food factor. The food density means and ranges are given along with the average percent biting response for each of the food treatment combinations. Percent biting increased with *Artemia* adult density at both levels of nauplii density and decreased

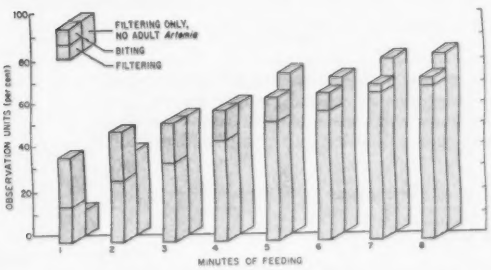

FIG. 1. Percentages of filtering and biting activity for each minute of the trial period. Front bars represent averages by minute for 42 trials in which fish were exposed to combinations of *Artemia* adults and nauplii. Rear bars represent averages by minute for 6 trials in which fish were exposed to nauplii alone. Average nauplii density was higher for the latter series of trials.

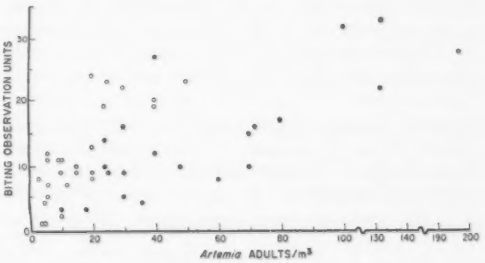

FIG. 2. The relation of biting observations to density of *Artemia* adults for 46 trials in which both adults and nauplii were present. Density of *Artemia* nauplii: ○, < 400,000/m³; ●, > 400,000/m³.

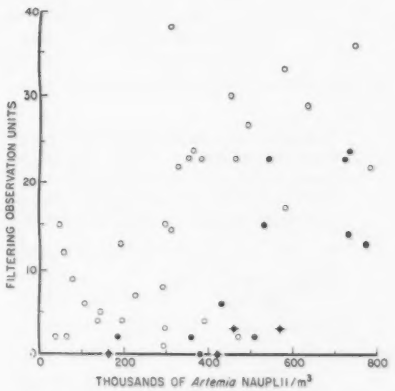

FIG. 3. The relation of filtering observations to density of *Artemia* nauplii for 46 trials in which both adults and nauplii were present. Density of *Artemia* adults: ○, < 40/m³; ●, > 40/m³; -+-, > 100/m³.

with nauplii density at both levels of adult density. An analysis of variance showed that only the two main effects were important, and that percent biting was largely associated with the density of *Artemia* adults ($F = 11.0$, df 1/20), but nauplii did have a discernible effect ($F = 1.58$, df 1/20), which would probably have been stronger if the average density of *Artemia* adults had been more nearly alike for the two treatment combinations in which adults were high. In any event, percent biting will be described as a function of *Artemia* adult density for broad ranges of nauplii density.

Trends of relative biting and filtering are shown by normal probability plots of percent biting (PB) on *Artemia* adult density for three different ranges of nauplii density (Fig. 4). Probit analysis was used to estimate the parameters of the fitted lines for suitably limited ranges, i.e., for values excluding 0 and 100% response. Individual points represent PB values for trials pooled in successive intervals of four *Artemia* adults/m³. Trials with nauplii densities below 100,000/m³ were excluded because they encompassed too narrow a range of *Artemia* adult density, and trials with adult densities above 100/m³ were excluded because a few would have produced responses of 100%, a nonexistent value on the probit scale.

The data for the highest range of nauplii density were judged to be inconclusive because the PB values obviously did not show a significant trend. The only distinguishable increase in response was the PB value for the highest *Artemia* adult density. The arrays for the other two ranges, however, do show good evidence of linear trends, and regressions for each can therefore be taken to represent cumulative normal distributions (Bliss 1967) with parameters $\hat{\mu}$ and σ, where $\hat{\mu}$ is the mean density of adults at 50% response and $\hat{\sigma}$ is the standard deviation. Values for these parameters are given in Table 2. The χ^2 values show that the array of PB values for the lowest

TABLE 1. Average percent biting for four treatment combinations of *Artemia* adult and nauplii density. Mean density and range of adults (A) and thousands of nauplii (N) is shown for each treatment combination.

Artemia adult density	*Artemia* nauplii density	
	Low	High
Low	42	24
	A 10(*4–15*)	11(*6–18*)
	N 242(*107–311*)	389(*325–465*)
High	79	69
	A 27(*20–40*)	35(*20–50*)
	N 219(*141–298*)	416(*360–484*)

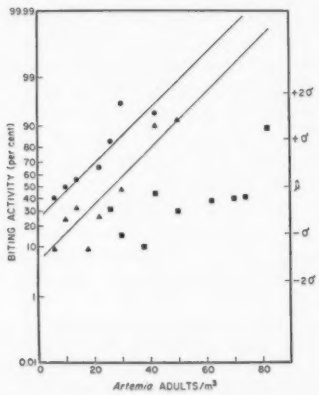

FIG. 4. Probit regressions of percent biting response on density of *Artemia* adults for three categories of *Artemia* nauplii density. *Artemia* nauplii density: ●, 100–300 thousand/m³; ▲, 300–500 thousand/m³; ■, > 500 thousand/m³. Mean and standard deviation of response are indicated at right.

TABLE 2. The normal cumulative distributions that describe the relation of percentage biting response to density of *Artemia* adults for three categories of *Artemia* nauplii density. $\hat{\mu}$ is mean and $\hat{\sigma}$ is standard deviation of the distributions. *n* is the number of 10-sec response units and N is the number of *Artemia* adult density classes in which they occurred. Significant χ^2 values indicate departure from normality.

Nauplii density range '000/m³	*n*	N	$\hat{\mu}$	$\hat{\sigma}$	χ^2
100–300	214	7	11.78±2.78	17.10±3.44	4.08
300–500	342	8	26.70±1.34	17.00±1.76	16.21[a]
500+	381	9	–	–	27.58[b]

[a] $P = 0.05$.
[b] $P = 0.01$.

range of nauplii density is acceptably normal, while that for the high range is not, and that for the middle range is uncertain. In view of the graphic evidence, the deviation from normality indicated for the middle range is probably attributable to inflation of variability, a not unexpected result where the experiment occurred over a long time and the results from individual trials were combined irrespective of the time element for analysis. Use of the uncorrected estimates of $\hat{\mu}$ and $\hat{\sigma}$ means only that the standard errors for each should be considered conservative.

The regression lines for the low and middle ranges of nauplii density, which have the same slope (0.59), and which represent normal cumulative functions that differ only in mean ($\hat{\mu}$), show that the proportion of feeding activity devoted to biting rather than filtering by small schools of anchovies increased as density of *Artemia* adults increased, and/or as density of nauplii decreased. The expected percent of biting activity can be estimated directly from Fig. 4 for any density of *Artemia* adults with *Artemia* nauplii assumed to be at a density of 200,000/m^3 or 400,000/m^3.

The above distributions define percent biting as an average for the school, but the average is based on summation over three positions in the school, and analysis by position indicates that there is a gradation of feeding response within the school. To evaluate the significance of position differences, however, it is necessary to test the hypothesis that variation in feeding activity with position is not associated with variation between observers. Since the positions were not occupied an equal number of times by each observer among all trials, the hypothesis was tested for 24 trials in which each observer was at each position eight times. The numbers of 10-sec intervals scored as biting (B), filtering (F), and zero (0) activity over the first 3 min is shown in Table 3 by position for all of these trials, and by observer for each position. Feeding activity differs markedly between positions ($\chi^2 = 74.6$), with biting higher than filtering at the front and filtering higher than biting at the middle and rear. Though not grouped as such in the table, differences between position for each observer show the same marked pattern. χ^2 values are 43, 44, and 52 (df = 4) for observers A, B, and C, respectively.

The χ^2 values for the three positions, as given in the table, show, on the other hand, that all three observers scored essentially the same distribution of biting, filtering, and zero observations for the front and rear positions. There is significant deviation from expected at the middle position, although all three observers did score more filtering than biting. Inequities in the average food situation represented by the eight trials for each observer were greater at the middle than at the front and rear positions, and may have been partly responsible for the higher deviations in this set. Variation at the middle position notwithstanding, it can be concluded from these tests that differences between positions are far greater than differences between observers.

The nature of the gradient in feeding activity is evident in probit regressions for each of the three school positions — front, middle, and rear — for

TABLE 3. Contingency tables and χ^2 values for relation of the number of 10-sec intervals scored as biting (B), filtering (F), and zero (0) feeding activity in 3 min to position of observation in the school, and to observer at each position. n = number of feeding trials in which each position was observed. df = degrees of freedom. Expected distributions are shown in parentheses.

Position	Observer	n	B	F	0	χ^2	df
Front	All	24	132	51	249	74.6***	4
Middle	All	24	59	174	199		
Rear	All	24	74	137	221		
			(88.3)	(120.7)	(223.0)		
Front	A	8	51	19	74	8.32	4
	B	8	42	10	92		
	C	8	39	22	83		
			(44.0)	(17.0)	(83.0)		
Middle	A	8	29	56	59	19.3***	4
	B	8	18	45	81		
	C	8	12	73	59		
			(19.7)	(58.0)	(66.3)		
Rear	A	8	28	50	66	7.14	4
	B	8	20	52	72		
	C	8	26	35	83		
			(24.7)	(45.7)	(73.7)		

trials in the 100,000–300,000 nauplii/m³ range (Fig. 5A) and for trials in the 300,000–500,000 nauplii/m³ range (Fig. 5B). The regressions were fitted to PB values calculated for each position for the same combinations of *Artemia* adult and nauplii densities for which the average PB values were calculated. For the lower nauplii range (Fig. 5A) no regression was calculated for the front position because five of the PB values were 100%. These and the two values shown for the front position, nevertheless, demonstrate that fish in the lead position consistently showed far higher percentages of biting than fish in following positions. For the higher range of nauplii density (Fig. 5B) the same phenomenon is evident but less pronounced. Here, however, the line for the middle position indicates that percent biting response became as strong in the middle as in the front position when *Artemia* adult density was high. The general pattern is clearly a gradation from higher percent biting at the front to lower percent biting at the rear with variations in the strength and intensity of gradient dependent on the relative abundance of the two sizes of organism in the water.

Contributions of Biting and Filtering to Ingestion Rate

Average ingestion rate for individuals in the school, and the contribution of *Artemia* adults and nauplii to this average, must depend on the rates at which the two sizes of organism are captured as well as on the ratios for the two associated feeding activities in the school. The relation of numbers captured to density for nauplii is suggested by equation 5 in Leong and O'Connell (1969). Those authors also described feeding rate for *Artemia* adults, but only for densities above 1000/m³. Feeding rate for low densities of adults can be estimated for simulated daylight conditions from the pilot study described under methods above. In 10 of the trials nauplii were essentially ignored by the fish, and the relation between *Artemia* adults in the water and in digestive tracts was

No./m³	6	6	8	8	12	18	100	100	1000	10,000
No./fish	1	1.5	2	3	4.7	8.3	19	25	95	78

The correlation is obvious, except that average number consumed was no higher for a density of 10,000/m³ than for a density of 1000/m³. This is consistent with the finding by Leong and O'Connell (1969) that number of *Artemia* adults consumed by the anchovy was not related to density over the range 1000/m³–25,000/m³. If the 10,000/m³ entry is excluded on the assumption that it is far above some inflexion point where feeding rate ceases to increase with density, the relation for the remaining nine pairs of values ($r = 0.97$) is described by the line

$$\text{Log } N = 0.82 \text{ Log } D - 0.36 \qquad (1)$$

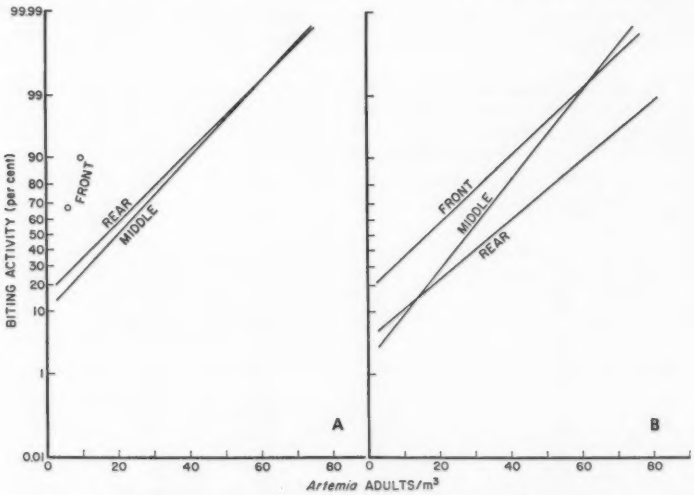

FIG. 5. Probit regressions of percent biting response on density of *Artemia* adults for front, middle, and rear positions in the school for trials with A, *Artemia* nauplii in the 100–300 thousand/m³ range, (No regression line is shown for the front position because 5 of the 7 points were off scale at 100%), and B, *Artemia* nauplii in the 300–500 thousand/m³ range.

where N = average number of *Artemia* adults consumed in 5 min, and D = average number of *Artemia* adults/m³ present in the water at the start of feeding.

Under the assumption that basic rates derived from equation 1 above and equation 5 in Leong and O'Connell (1969) are effective in proportion to the ratios for the two kinds of feeding activity in the school, the products of these basic rates and ratio values for the densities present should provide a partial rate for each size of organism. The sum of the partial rates, expressed in comparable units, will be the average total rate for the density combination. Basic, partial, and total rates are shown for four density combinations in Table 4. The rates are expressed as the milligram dry weight that would be consumed in 1 min by a fish weighing 5 g (average weight of fish in pilot study). The four density combinations are based on the midpoints of the nauplii density ranges for which probit regressions were calculated and on the adult densities indicated by those regressions (Fig. 4) for 50 and 99% biting activity.

The values in Table 4 indicate that when dry weight concentration of *Artemia* adults in the water is 2% of the total concentration, the basic rates are similar for the two sizes of organism and particulate and filter feeding activity are equal. Under these circumstances the ingestion rate for both sizes together, or total rate, is no greater than would be possible by filtration alone on the nauplii. However, when the dry weight concentration of *Artemia* adults is in the order of 5.5–8% of the dry weight of adults and nauplii together, the basic rate for *Artemia* adults is approximately double that for nauplii. Under these circumstances total ingestion rate is approximately double that possible by filtration alone, and filter feeding contributes little to total ingestion.

The possibilities of ingestion rate, of course, are not limited to the combinations illustrated. Total ingestion rate would presumably be intermediate between those for 50 and 99% biting activity if density of larger organisms were intermediate between those that support such levels of biting. Ingestion rate might also be more than double the filtration potential if the density of larger organisms were markedly greater than necessary for the 99% level of biting activity. Also, ingestion rates might be somewhat lower, or the concentrations of large organisms necessary to sustain them somewhat higher than indicated, if escapement of larger crustaceans in the sea is appreciable. Though biting may tend to counteract escapement, the calculations are based on *Artemia* adults, which appear to have no effective escape response.

Interrelation of Biting and Filtering in the Sea

Although the anchovy probably relies on filter feeding for a steady supply of food in the sea, this supply may often fail to sustain the daily nutritional requirement, as already hypothesized. The experiments described here suggest that biting could be an augmenting activity of some consequence, depending on the size composition of the plankton. O'Connell (1971) showed that plankton pump samples from surface waters off southern California vary greatly in relative abundance of large and small crustaceans. Of the constituents described, small copepods, with an average dry weight equivalent of 0.0025 mg, and euphausiids, with average dry weight equivalents of 0.042 mg for day samples and 0.293 mg for night samples, most closely approximate the *Artemia* nauplii and adults used in the laboratory

TABLE 4. Estimated ingestion rates for density combinations of *Artemia* adults and nauplii at which biting activity is 50 and 99% of total feeding activity.

	Low nauplii density				High nauplii density			
Percent biting activity	50		99		50		99	
Organism type	Nauplii	Adults	Nauplii	Adults	Nauplii	Adults	Nauplii	Adult
Density no./m³	200,000	12	200,000	52	400,000	27	400,000	66
Dry wt mg/m³	290	6	290	26	580	13.5	580	33
Adult % of total dry wt		2.0		8.2		2.3		5.4
Ingestion rates (mg dry wt/min) for above densities								
Basic	0.49	0.34	0.49	1.1	0.73	0.65	0.73	1.4
Partial	0.24	0.17	0.01	1.1	0.37	0.33	0.01	1.4
Total		0.41		1.1		0.70		1.4

study. They also constituted the bulk of the dry weight of the samples. Averages for five cruises indicated that euphausiids were 3–5% of the dry weight of both groups during the day and 21–66% at night. These percentages suggest that anchovy feeding in surface waters would be chiefly filtering in the daytime and chiefly biting at night, with ingestion rate far exceeding the filtration potential in the latter period.

However, the small laboratory school can scarcely represent more than the leading edge of many schools in the sea. Since percentage of biting diminished noticeably in following positions in a small school, it is possible that diminution extends to a complete lack of opportunity for biting activity for most of the fish in large, compact schools. This would result in a lower capture rate of the larger crustaceans and a lesser elevation of total digestion rate, on the average, than might be expected for a small school exposed to the same relative concentrations.

There is circumstantial evidence to suggest, on the other hand, that the anchovy schools more loosely when larger food organisms are abundantly available. In the laboratory experiments the fish schooled under all trial circumstances, but in the presence of the higher densities of *Artemia* adults, where initial activity was largely biting, they appeared to swim faster and be more widely separated than in circumstances where most of the activity was filtering. Hobson (1968), on the basis of extensive field observations, found that the flatiron herring, *Harengula thrissina*, remained inshore in dense schools during the day and moved offshore, possibly in looser aggregations, to feed at night when shrimp-like crustaceans were most abundant in midwaters. He cited other clupeids that have been observed to break up into smaller, more loosely associated feeding groups at night. Such a behavior pattern, which might well apply to the northern anchovy, would operate to improve the average rate of encounter with larger crustaceans, and thereby raise the average rate of ingestion in respect to the filtration potential, although perhaps still not as much as might be expected for a small laboratory school.

Whatever the daily feeding cycle of the anchovy, it appears that opportunities for biting activity would be greatest in dim light — either at depth during the day, or near the surface at night. Because of strong vertical migration, high densities of euphausiids are common only under these conditions, and O'Connell (1971) has shown that the larger copepods, which may also elicit biting, have a vertical migration pattern similar to that of the euphausiids. Small copepods, on the other hand, showed evidence of only a slight nighttime increase at the surface.

Feeding by biting, because it is so obviously dependent on visual perception of individual organisms, may not seem compatible with low nighttime levels of illumination, but there is some evidence to the contrary. Hobson (1968) commented that some authors greatly underestimate the extent to which vision can be used at night by both predators and prey. Hunter (1968) showed that juvenile jack mackerel (*Trachurus symmetricus*) obtained 50% of the usual daytime ration when feeding by biting on *Artemia* adults at a light intensity as low as would occur near the surface on a full moonlit night. He noted, also, that more visible energy may exist in the sea than his calculations indicate. Blaxter (1964) listed a number of "visual" feeders that stopped feeding at similarly low light intensities. In regard to the northern anchovy, O'Connell (1963) showed on anatomical grounds that this species has a retina that is probably better adapted

TABLE 5. Hours of feeding necessary for an anchovy weighing 5 g to obtain its daily nutritional requirement (74 mg dry wt) from observed nighttime plankton concentrations for four different percentages of particulate feeding activity. Rules separate the values at 12 and 24 hr.

Zooplankton concentration mg/m³ dry wt	% samples	Hr of feeding			
		Filtering only	50% biting	75% biting	99% biting
10	27	84	84	56	42
20	17	42	42	28	21
30	41	28	28	19	14
40	10	21	21	14	11
50	5	17	17	11	9

than that of the jack mackerel for dim-light vision.

From all of the above evidence it seems highly probable that the anchovy can feed by biting at night, and by so doing effectively exceed the limitations of filtering. Loukashkin's (1970) finding that euphausiids and large copepods were the most important items in stomach contents of the anchovy tends to confirm this view.

Leong and O'Connell (1969) evaluated the food potential of zooplankton concentrations in the sea for the anchovy by estimating the hours of filtering necessary to obtain the daily nutritional requirement. Table 5 suggests the way in which different percentages of biting activity might effect this index of food potential, where the different percentages of biting imply that a given concentration is composed of different though undefined proportions of large and small organisms. The percentage distribution for dry weight concentrations is based on the night samples from five plankton pump cruises (O'Connell 1971). Hours of filtering for each dry weight class were calculated on the assumptions that a 5 g anchovy requires 74 mg dry weight of food per day and filters water at the rate of 1.46 liters/minute (Leong and O'Connell 1969). Hours of feeding for percentages of biting were calculated on the basis of the relations suggested in Table 5. That is, ingestion rate is no different for plankton that elicits 50% biting than for plankton that elicits filtering only, but varies proportionately from a factor of one at 50% biting to a factor of two at 99% biting. Feeding duration is inversely proportional to feeding rate.

The calculated values, which are separated by lines at 12 and 24 hr in the table, indicate that with low biting activity only 15% of the area sampled would have provided the anchovy with its nutritional requirement in one day. The same fraction of the area would have provided the daily requirement in less than 12 hr if the plankton concentrations supported relatively high average percentages of biting. If feeding extended over more than 12 hr with a high percentage of biting most of the time, more than half of the area could have provided the required nutrition. The anchovy may capture large organisms less effectively in relation to density at night than indicated earlier for simulated daylight conditions, but given the high ratios of euphausiid to small copepod dry weight in night samples, some average percentage of biting well above 50% seems entirely possible. Availability of the daily nutritional requirement would also tend to be widened if the anchovy utilizes phytoplankton along with zooplankton. These considerations suggest that plankton is usually adequate for the nutritional needs of the anchovy in a large part of the surface waters off southern California.

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Identification of Major British Columbia and Alaska Runs of Even-Year and Odd-Year Pink Salmon from Scale Characters

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BILTON, H. T. 1971. Identification of major British Columbia and Alaska runs of even-year and odd-year pink salmon from scale characters. J. Fish. Res. Bd. Canada 29: 295–301.

The present study indicates to what extent the various even- and odd-year pink salmon runs originating in British Columbia and Alaska may be identified from two scale characteristics. Discriminant function analysis indicates that for both the even- and odd-year runs in most instances only small proportions of each of the runs could be correctly identified to their specific place of origin. The only exceptions were the Fraser River and Aleutians runs where more than half were correctly classified to their place of origin. However, quite large proportions of most of the major even- and odd-year runs from the British Columbia and Alaska regions could be correctly classified to their region of origin.

An analysis, using a simple regression line method, of fish grouped into two regions rather than by run indicates that quite large proportions of fish from both even- and odd-year runs from the British Columbia and Alaska regions could be correctly classified to their region of origin. It would appear that the simpler analysis was equally as good as the discriminant function analysis of the individual runs for classifying fish to their region of origin on the basis of only two scale characters.

BILTON, H. T. 1971. Identification of major British Columbia and Alaska runs of even-year and odd-year pink salmon from scale characters. J. Fish. Res. Bd. Canada 29: 295–301.

La présente étude démontre jusqu'à quel point on peut, à l'aide de deux caractéristiques des écailles, identifier les montaisons de saumons roses d'années paires et impaires en Colombie britannique et en Alaska. L'analyse des fonctions discriminantes révèle que les montaisons d'années paires aussi bien que d'années impaires peuvent, dans la plupart des cas, être identifiées correctement quant au lieu spécifique d'origine. Les seules exceptions sont celles du fleuve Fraser et des Aléoutiennes, ou plus de la moitié des montaisons fut assignée au lieu d'origine. Par ailleurs, un fort pourcentage de la plupart des principales montaisons d'années paires et impaires en Colombie britannique et en Alaska a pu être classé correctement suivant la région d'origine.

Une analyse, par simple méthode de ligne de régression, des saumons roses groupés en deux régions plutôt qu'en montaisons démontre qu'un important pourcentage de saumons de montaisons d'années paires et impaires en Colombie britannique et en Alaska peut être classé correctement suivant la région d'origine. Il semble donc qu'une analyse plus simple est tout aussi efficace que celle des fonctions discriminantes pour classer les poissons suivant la région d'origine, sur la base de deux caractères scalaires seulement.

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THE pink salmon (*Oncorhynchus gorbuscha*) is common along the whole coast of British Columbia and Alaska to the Bering Sea. It spawns in streams usually near tidal waters from late September to early November. The eggs are buried in gravel and generally hatch early in the following spring. The resulting fry go to sea and reach maturity at 2 years of age (age 0.1).[1]

In many areas there is a large spawning run in 1 year and a small one in the next. Elsewhere the runs of successive years may be approximately equal in size. In some streams there are no runs at all in al-

[1]The European system of age designation (Koo 1962) is used in this report. The first digit indicates the number of annuli formed in fresh water and the second digit indicates the number of annuli formed while the fish was in the ocean.

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ternate years. In the southern part of British Columbia, the large runs have been in the odd years while in the northern part the large runs have tended to be in the even years.

Seasonal variation in growth of fish is reflected in the spacing of circuli on the scale. When growth slows in autumn and winter, circuli tend to grow closer together, forming closely spaced bands (in this paper they are referred to as annual rings). During the following spring or summer, the distance between circuli increases again as rapid growth is renewed. The last narrowly spaced circulus of the annual ring preceding the first, more widely spaced circulus is referred to here as the "annulus" (Fig. 1).

As scale growth is closely related to the growth of the fish, the patterns of circuli and annuli reflect the past history of growth of the individual. Growing conditions and growth of pink salmon vary widely while they are in the ocean. It is reasonable to expect that the scales of pink salmon would reflect differences in the ocean environments.

There have been a number of studies of scale characteristics to distinguish runs of pink salmon. Ishida and Miyaguchi (1959) attempted to identify the area of origin of pink salmon caught on the high seas in 1957. They observed differences in numbers of circuli and measurements between fish originating from central and western Alaska and southeastern Alaska and British Columbia. Other studies have indicated a west to east cline in first year circulus counts and in the spacing of the circuli, from Washington state to the U.S.S.R. coast (Amos et al. 1963; Pearson 1963, 1964, 1966a, b; Neave et al. 1967). Circulus counts of pinks taken on the high seas were compared with those of pinks from various shore areas in attempts to estimate the high seas distribution of Asian, northern Alaskan, and central British Columbia pink salmon.

The purpose of the present report is to indicate to what extent the various major runs originating from British Columbia and Alaska in the even- and odd-years can be identified from two scale characteristics. This report is based upon the more detailed data given in Bilton (MS 1971).

Materials and Methods

A total of 7281 even-year and 5273 odd-year pink scales from various North American coastal areas collected during 1956–64 were examined. These samples were obtained by governmental agencies of Canada and the United States (Fisheries Research Board of Canada, Bureau of Commercial Fisheries, Alaska Department of Fish and Game) from commercial fishery catches in fishing areas close to spawning grounds. Samples were obtained from most of the major producing areas in British Columbia, southeastern Alaska, and northwestern Alaska for nearly all 9 years of the study.

For several British Columbia runs samples were obtained throughout each spawning migration but for others, from British Columbia and Alaska, samples were obtained only for a day or two near the peak of abundance. The various sampling locations are shown in Fig. 2.

Scales were taken from the part of the body just below the insertion of the dorsal fin and two or three rows above the lateral line (INPFC 1955). Scales obtained were mounted on gummed cards, and impressions of the scale surface were made in cellulose acetate cards using methods similar to those described by Clutter and Whitesel (1956).

Scale Examination

The image of the scale impression was projected, at a magnification of 100, onto a sheet of graph paper divided into 1-mm squares. A Leitz Prado-X 123 microprojector equipped with plano lenses was used. The graph paper was oriented so that one of the lines on the paper lay along the longest axis of the scale from the focus to the edge. The outer edge of the image of each circulus, from the scale focus to the annulus, was then marked on the graph paper. Because many circuli are broken or branch, only those circuli which continued more or less intact within a distance of 1.0 cm on both sides of the long axis of the projected image were counted. A diagrammatic representation of a section near the long axis is given in Fig. 3. This illustrates the criteria for inclusion or exclusion of circuli for measurements. The annulus was also marked on the graph sheets.

The following counts and measurements were made from scales of pinks sampled from various major runs in British Columbia and Alaska. All measurements were made along the longest anterior axis of the scale (Fig. 1): C_1 = the number of circuli in the first ocean zone from the scale focus to the ocean annulus; A_1 = width of the first ocean zone from the scale focus to the ocean annulus. In this study the data were combined by sex and brood year but not by even- and odd-year run.

Statistical Analyses

Frequency tables of the measurements of scale characters of the fifteen runs[2] indicated differences among a number of runs. A simultaneous comparison of the scale characters was required to achieve the best means of identifying the runs from their scale characters. Thus, the discriminant function analysis was used in the present report, using the scale characters listed in this report,

[2]For the purposes of this report, a run is defined as a group of fish which originate either from one, or a group of major systems in a geographical area. For example, all fish from the Fraser River and all fish from the Bristol Bay area are here defined as runs. No attempt was made to identify individual groups of fish from different river systems in the Bristol Bay area.

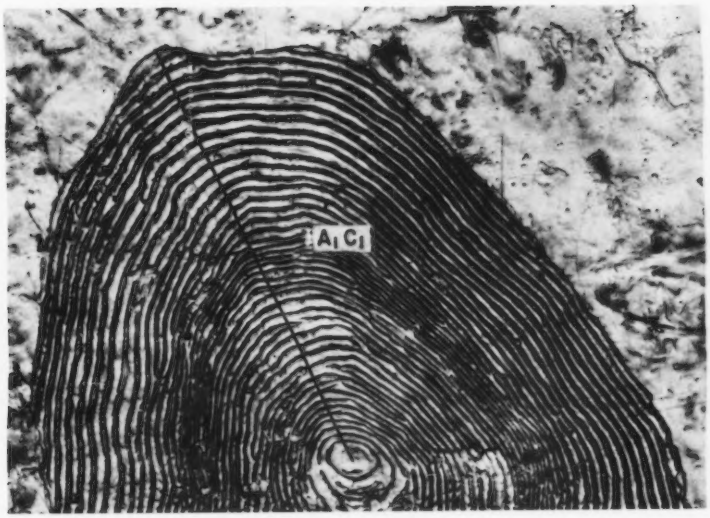

FIG. 1. Scale from an adult pink salmon showing the ocean annulus (A_1, C_1).

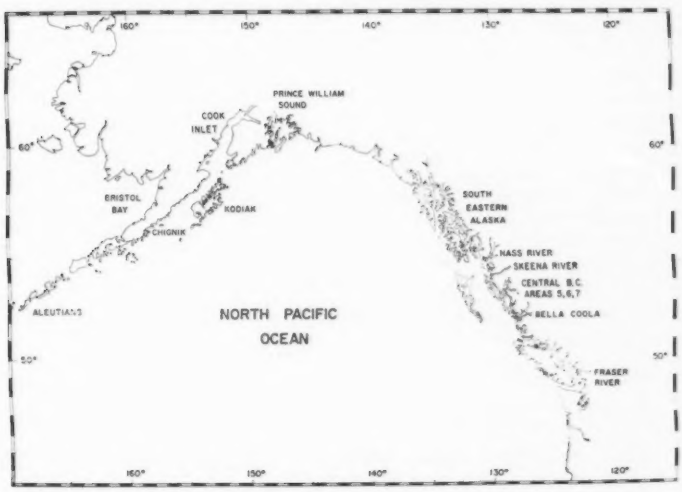

FIG. 2. Map showing locations of coastal sampling areas.

Bilton — J. Fish. Res. Bd. Canada

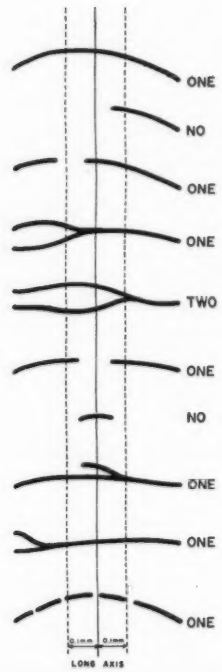

FIG. 3. Diagrammatic representation of a section of a scale within 0.1 mm of the long axis, showing "breakage" and "branching" of circuli and indicating the criteria for inclusion of circuli in counts and measurements. "One" and "two" indicate the number of circuli that would be included in counts and for which positions would be marked for measurements. "No" indicates that circulus would not be included in counts and that the position of its image would not be marked for measurement (Tanaka et al. 1969).

as well as one ratio obtained by combining scale characters, i.e., A_1/C_1.

Cooley and Lohnes (1962) describe discriminant analysis as "a procedure for estimating the position of an individual on a line that best separates classes or groups." The estimated position is obtained as a linear function of the individual's test scores. Correct use of the linear discriminant function requires the following assumptions: (a) frequency distributions, of the data are multivariate normal; (b) the data have common variance–covariance matrices; and (c) each individual to be classified is from one of the groups to which individuals are being assigned.

These assumptions were tested and they seemed to be met except for homogeneity of dispersions. However, according to Cooley and Lohnes (1971) "many research workers prefer to ignore the issue of the homogeneity of group dispersions on the grounds that the test of H_2 (equality of means) is probably fairly robust under departures from its assumptions. Also these multivariate tests are quite powerful, so research on large samples is quite likely to lead to a rejection of H_1 (homogeneity of dispersions) with some consequent embarrassment to a manova theory for the data". Furthermore, the robustness of the test is confirmed to some extent by the similarity of results on the test samples to the results on the test samples used to derive the functions.

Functions were derived by even- and odd-year groups for each of the runs. These functions were obtained from the scale measurements of 40 fish randomly selected over a period from 1 to 5 years for the even-year group and over a period from 1 to 4 years for the odd-year group. In addition, samples of scale characters of other fish of each group, from each of the same runs, in each of from 1 to 5 years were used to test the discrimination for each of the runs. Discriminant function analysis was carried out to: (a) estimate how well the derived functions for each run could correctly classify those same individuals used to derive the functions, and (b) estimate how well the derived functions could correctly classify other individuals in samples from each run. The results of these analyses indicate the percent of fish in samples from each run that were correctly identified and the percent that were misclassified to one or more of the other runs.

Discriminant analysis for groups of runs was also tried in an attempt to improve the ability to discriminate. First, the original test samples from the fifteen runs were combined into four on a judgmental basis as follows: group 1, Fraser River and Bella Coola; group 2, central B.C. areas 5, 6, 7, and Skeena and Nass rivers; group 3, southwestern Alaska; group 4, Prince William Sound, Cook Inlet, Kodiak, Chignik, Aleutians, Alaska Peninsula, and Bristol Bay. Second, the distributions were then combined into two groups; the Alaska region including all Alaskan runs, and the British Columbia region including all B.C. runs with the Nass River being omitted because of the possibility that the samples from this run could also contain fish from southeastern Alaska. Scatterplots of the two variables (C_1 and A_1) were prepared for each region. Regression lines were calculated. As a simple discriminator, a line was drawn for each region halfway between the regression lines. The numbers correctly classified to region were counted and the percentages computed.

Results

British Columbia Even- and Odd-Year Pink Runs

The proportion correctly classified, when each fish in the samples used to derive the functions for each run was tested with the functions (see Bilton MS 1971 for details).

For the even-year runs the percent correctly identified varied from a low of 10% for Nass River and central B.C. fish to a high of 67.5% for Bella Coola fish. Twenty and thirty percent of the Skeena and Nass River fish, respectively, were misclassified as originating from Cook Inlet. In general, the percentages of the runs correctly identified was quite low (overall average of 36.8%). However, when the percentages of the even-year British Columbia runs that were correctly identified are added to the percent of those incorrectly identified but originating from other British Columbia runs, the total percent identified as originating from the British Columbia region[3] is quite high (ranging from 62.5% for the Nass run to 97.5% for the Bella Coola run).

For the odd-year runs the percent correctly identified varied from a low of 5.0% for central B.C. fish to a high of 80.0% for Fraser River fish. In general, the percentage of the odd-year runs was low (overall average of 33.5%). However, the total percent of odd-year British Columbia runs correctly identified as originating from the British Columbia region was high (ranging from 82.5% for the Skeena and Nass pinks to 100.0% for the Fraser River pinks). These results and those for Alaska suggested the use of regions rather than runs as discussed later.

The proportion correctly classified when fish in other samples from each of the same runs were tested with the functions (see Bilton MS 1971 for details).

The percentages of British Columbia pinks in each of the even-year and odd-year runs over 3–5 years that were correctly identified to a specific run, and the total percentages correctly classified as originating from British Columbia are given in Table 1.

For the even-year runs Bella Coola and Skeena River fish had the highest percentages (27.2–65.2%; 35.9–51.1%, respectively) correctly classified. Nass run pinks had low percentages (3.3–24.8%) correctly classified. Their scale characters tended to be similar to those of the Bella Coola and Skeena River and to southeastern Alaska and Prince William Sound runs in Alaska. Nearly all of the other central B.C. runs were incorrectly identified as originating from the Bella Coola, Skeena River, and Nass River

[3]The British Columbia region: All runs within British Columbia.

TABLE 1. The percentages of even- and odd-year pinks in each of the British Columbia runs over 3–5 years, correctly identified to a specific run, and the total percentages correctly classified as originating from B.C. and Alaska.

Source	Year	No. Years	N[a]	% correctly classified	Most incorrect identifications classified as	% classified as B.C.	% classified as Alaska
Fraser River	Even	–	–	–	–	–	–
	Odd	3	208	52.6–72.4	Bella Coola, Central B.C., Skeena River	97.4–100.0	0.0–2.6
Bella Coola	Even	5	757	27.2–65.2	Skeena R., Nass R., Prince William Sd.	86.0–92.0	8.0–14.0
	Odd	3	249	4.0–9.2	Fraser R., Skeena R. Nass R.	94.7–98.9	1.1–5.3
Other Central B.C.	Even	3	858	0.7–3.5	Bella Coola, Skeena R., Nass R., Prince William Sd.	70.4–84.0	15.7–29.6
(areas 5, 6, 7)	Odd	3	843	3.0–8.0	Fraser R., Skeena R., Nass R., Bella Coola	86.8–92.6	7.4–13.2
Skeena River	Even	5	448	35.9–51.1	Bella Coola, Nass R., Prince William Sd.	69.3–84.8	15.2–30.7
	Odd	4	361	15.4–35.6	Fraser R., Nass R., Prince William Sd., Cook Inlet	66.7–94.5	5.5–33.3
Nass River	Even	4	334	3.3–24.8	Bella Coola, Skeena R., southeastern Alaska Prince William Sd.	49.3–75.6	24.4–50.7
	Odd	4	302	34.4–54.5	Fraser R., Skeena R., Prince William Sd., Cook Inlet	65.4–94.5	5.5–34.6

[a]Number of individuals in samples.

runs. However, none of these latter runs were incorrectly identified as originating from the other central B.C. runs. Perhaps fish caught, and designated as other central B.C. runs were actually of Bella Coola, Skeena River, and Nass River origin moving through these areas en route to their respective river systems.

Although in most instances large percentages of the even-year runs could not be correctly classified from their scale characters, quite large percentages of the runs were correctly classified as originating from the British Columbia region. This was particularly so for the Bella Coola run where from 86.0 to 92.0% was correctly classified. For the other central B.C. runs, Skeena River, and Nass River runs the percentages were lower, ranging from 49.3 to 84.8%.

Among the odd-year runs, Fraser River pinks had the highest percentages (52.6–72.4% correctly classified. Low percentages (4.0–9.2%) of Bella Coola, Skeena River (15.4–35.6%), and Nass River (34.4–54.5%) fish were correctly identified. Like the even-year, other central B.C. runs, nearly all of odd-year other central B.C. runs were incorrectly identified as originating from the Fraser River, Bella Coola, Skeena River, and Nass River runs. The low percentages (4.0–9.2%) of Bella Coola fish correctly identified was due to the fact that their scales tended to be similar to those of the Fraser River (from 48.0 to 74.7% were incorrectly identified as Fraser River fish).

Even though, in most instances, large percentages of the odd-year runs could not be correctly classified from their scale characters, quite large percentages of the runs were correctly classified as originating from the British Columbia region. Fraser River and Bella Coola runs had the highest percentages (94.7–100.0%) correctly classified as originating from British Columbia. For the Skeena and Nass river runs the percentages were lower, ranging from 65.4 to 94.5% correctly classified.

In general, the percentages correctly classified as originating from British Columbia, were higher among the odd-year runs than among the even-year runs.

ALASKA EVEN- AND ODD-YEAR PINK RUNS

The proportion correctly classified, when each fish in the samples used to derive the functions for each run was tested with the functions (see Bilton MS 1971 for details).

For the even-year runs the percent correctly identified was low (overall average of 26.2%). Runs from the Aleutians and Bristol Bay had the highest percentages at 65.0 and 50.0, respectively. The total percent of even-year Alaska runs correctly identified as originating from the Alaska region[4] was quite high

[4]Alaska region: All runs within southeastern, central, western, and northern Alaska.

(ranging from 70.0% for the Prince William Sound run to 100.0% for the Chignik and Aleutian runs) except for those from Southeastern Alaska which had 57.5%. In the latter, 35% were misclassified as originating from the Nass River.

For the odd-year runs the percent correctly identified was low (overall average of 31.2%). Runs from Prince William Sound, Kodiak, and the Alaska Peninsula had the highest percentages, 67.5, 37.5, and 35.0, respectively. The total percent of odd-year Alaska runs correctly identified as originating from the Alaska region was quite high (ranging from 62.5% for the southeastern Alaska run to 97.5% for the Kodiak run).

The proportion correctly classified when fish in other samples from each of the same runs were tested with the functions (see Bilton MS 1971 for details).

The percentages of Alaska pinks in each of the even-year and odd-year runs over 1–5 years that were correctly identified to a specific run, and the total percentages correctly classified as originating from Alaska are given in Table 2.

For the even-year runs, Aleutian fish had the highest percentages (69.9–75.0%) correctly classified while those from southeastern Alaska (1.6–8.8%); Kodiak (0.0–2.2%), and the Alaska Peninsula (0.0–2.1%) had the lowest. Misclassified fish were identified as originating from the Bella Coola, Skeena River, Nass River in British Columbia and in many of the Alaskan runs.

In most instances quite large percentages of the even-year runs were correctly classified as originating from the Alaska region. The percentages correctly classified from the Alaska region ranged from 46.9 to 100.0%. Of all the runs, Cook Inlet, Aleutians, Alaska Peninsula, and Bristol Bay pinks had the highest percent correct classifications (95.7–100.0%). Those from southeastern Alaska had the lowest percentages (46.9–74.9%) correctly classified to region.

Among the odd-year runs, Prince William Sound pinks had the highest percentages (43.7–48.3%) correctly classified. Those from southeastern Alaska had the lowest percentages (0.0–4.0%) correctly classified. Misclassified fish were identified as originating from runs in British Columbia and Alaska.

For the odd-year runs pinks, the percentages correctly classified as originating from the Alaska region, ranged from 20.3 to 100.0%. Of all the Alaska runs, Aleutians pinks had the highest percent cor-

TABLE 2. The percentages of even- and odd-year pinks in each of the Alaska runs over 1–5 years, correctly identified to a specific run, and the total percentages correctly classified as originating from B.C. and Alaska.

Source	Year	No. Years.	N[a]	% correctly classified	Most incorrect identifications classified as	% classified as B.C.	% classified as Alaska
Southeastern Alaska	Even	4	1225	1.6–8.8	Skeena R., Nass R., Bella Coola, Chignik, Bristol Bay	25.1–53.1	46.9–74.9
	Odd	3	741	0.0–4.0	Fraser R., Skeena R., Nass R., Prince William Sd., Cook Inlet	31.3–79.7	20.3–68.7
Prince William Sound	Even	2	95	25.6–76.9	Skeena R., southeastern Alaska, Chignik, Bristol Bay	19.5–23.1	76.9–80.5
	Odd	2	261	43.7–48.3	Skeena R., Nass R., Cook Inlet, Kodiak	17.3–32.7	67.3–82.7
Cook Inlet	Even	5	669	0.0–33.0	Prince William Sd., Chignik, Aleutians, Bristol Bay	0.0–4.3	95.7–100.0
	Odd	3	459	7.0–21.1	Skeena R., Nass R., Prince William Sd., Kodiak, Aleutians, Alaska Peninsula	0.5–25.0	75.0–99.5
Kodiak	Even	5	662	0.0–2.2	Prince William Sd., Chignik, Aleutians, Bristol Bay	1.1–12.2	87.8–98.9
	Odd	3	598	31.7–44.0	Prince William Sd., Cook Inlet, Aleutians, Alaska Peninsula	1.5–13.4	86.6–98.5
Chignik	Even	1	60	46.7	Prince William Sd., Bristol Bay	5.0	95.0
	Odd	–	–	–	–	–	–
Aleutians	Even	3	717	69.9–75.0	Cook Inlet, Chignik, Bristol Bay, Kodiak, Alaska Peninsula	0.0–2.3	97.7–100.0
	Odd	1	72	31.9		0.0	100.0
Alaska Peninsula	Even	5	783	0.0–2.1	Prince William Sd., Chignik, Aleutians, Bristol Bay	0.0–3.9	96.1–100.0
	Odd	4	739	11.1–22.5	Prince William Sd., Cook Inlet, Kodiak, Aleutians	0.4–5.9	94.1–99.6
Bristol Bay	Even	3	193	26.9–36.5	Chignik, Aleutians	0.0–2.4	97.6–100.0
	Odd	–	–	–	–	–	–

[a]Number of individuals in samples.

rect classifications (100.0%). Those from southeastern Alaska had the lowest percentages (20.3–68.7%) correctly classified. For the other runs the percentages ranged from 67.3 to 99.6% correctly classified.

In general, there was little difference in the percentages correctly classified as originating from Alaska, among the even-year runs and the odd-year runs.

EVEN- AND ODD-YEAR PINKS FROM BRITISH COLUMBIA AND ALASKA COMBINED TO FOUR GROUPS, AND THEN TO TWO GROUPS, THE BRITISH COLUMBIA AND ALASKA REGIONS.

Discriminate analysis was unsuccessful in both the even- and odd-years in separating the four groups. This was probably due to lack of homogeneity of dispersions and to inadequate separation of group means.

Results of combining the distributions into the British Columbia and Alaska regions in the even- and odd-years indicated the relations between the two variables (C_1 and A_1) were similar for the two regions:

Even-years	Regression of C_1 on A_1	Correlation coefficient (r)
British Columbia	$\hat{C}_1 = 27.38 + 0.19(A_1 - 90.95)$	0.725
Alaska	$\hat{C}_1 = 23.09 + 0.18(A_1 - 94.56)$	0.675
Old-years		
British Columbia	$\hat{C}_1 = 28.88 + 0.16(A_1 - 101.61)$	0.726
Alaska	$\hat{C}_1 = 24.18 + 0.20(A_1 - 100.85)$	0.706

The percentages correctly classified to region on the basis of a line drawn for each region halfway between the above regression lines were as follows:

True Region		Classified Region: British Columbia	Alaska	Total
Even-years British Columbia	No.	169	21	190
	%	88.9	11.1	100
Alaska	No.	40	240	280
	%	14.3	85.7	100
Total	No.	209	261	470
Odd-years British Columbia	No.	166	21	187
	%	88.8	11.2	100
Alaska	No.	24	136	160
	%	15.0	85.0	100
Total	No.	190	157	347

The results indicate that over 80% of the fish originating from the British Columbia and Alaska regions were correctly classified to their region of origin. Thus the discrimination from this simple analysis by region was much better than was obtainable for individual runs.

Conclusions

The results of this study indicate that quite large proportions of most of the major even- and odd-year runs from the British Columbia and Alaska regions could be correctly classified to their region of origin. Thus it is probable that quite high proportions of fish caught on the high seas of unknown origin could be classified to region of origin on the basis of their scale characters.

In most instances only small proportions of each of the runs could be correctly identified to their specific place of origin from their scale characters. The only exceptions were the Fraser River and even-year Aleutians runs. It would appear in most instances that only small proport ons of fish caught on the high seas of unknown origin could be classified to specific runs in the British Columbia and Alaska regions.

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Prolactin and Growth Hormone Concentrations in the Serum and Pituitary Gland of Adult Migratory Sockeye Salmon (*Oncorhynchus nerka*)

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McKeown, B. A., and A. P. van Overbeeke. 1972. Prolactin and growth hormone concentrations in the serum and pituitary gland of adult migratory sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Bd. Canada 29: 303–309.

When sockeye salmon entered the Fraser River the prolactin content of the serum and the pituitary gland was reduced by 27 and 36%, respectively. During migration to the spawning grounds the serum concentration increased considerably (81%), while the pituitary concentration was gradually restored to that of the first seawater sample. Serum concentration of growth hormone gradually increased during the migration (29%), while growth hormone in the pituitary glands initially decreased (13%) then increased (12%) as the fish approached the spawning grounds. The changes in prolactin concentrations appear to be related to a change in salinity, whereas growth hormone changes were unaltered at this time.

McKeown, B. A., and A. P. van Overbeeke. 1972. Prolactin and growth hormone concentrations in the serum and pituitary gland of adult migratory sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Bd. Canada 29: 303–309.

Au moment de l'entrée des saumons sockeye dans le fleuve Fraser, la teneur en prolactine sérique et hypophysaire baisse de 27 et 36% respectivement. Au cours de la migration vers les frayères, la teneur sérique augmente considérablement (81%), alors que la teneur hypophysaire retourne graduellement au niveau du premier échantillon d'eau salée. La concentration sérique de l'hormone de croissance augmente au cours de la migration (29%), alors que dans l'hypophyse, cette hormone diminue d'abord (13%), puis augmente (12%) au moment où le poisson s'approche des frayères. Les variations de la teneur en prolactine semblent être liées à la salinité, alors qu'à ce stade-ci, les variations de l'hormone de croissance ne sont pas affectées.

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There is evidence that antibodies to mammalian pituitary hormones cross-react with the analogous hormones of the pituitary gland of bony fishes. This has been shown for prolactin (Emmart et al. 1966; Emmart and Mossakowski 1967; Emmart 1969; McKeown and van Overbeeke 1969, 1971; Aler 1970), growth hormone (Hayashida 1969, 1970; Hayashida and Lagios 1969; McKeown and van Overbeeke 1971), and corticotrophin (McKeown and van Overbeeke 1969, 1971). Both immunohistochemical and immunochemical techniques were used in these investigations.

Radioimmunoassay techniques have been successfully applied in situations where all hormone antigens involved were mammalian. To our knowledge, no reports concerning the application of radioimmunoassays in quantitative determinations of non-mammalian pituitary hormones have been published.

We decided to use this technique in our investigations concerning the hormonal activity of the pituitary gland of sockeye salmon (*Oncorhynchus nerka*). This report concerns changes in concentrations of prolactin and growth hormone in both the pituitary gland and serum, as the salmon migrate from the ocean to the spawning grounds. These two hormones cross-react with antibodies to corresponding ovine hormones (McKeown and van Overbeeke 1971). The functions of prolactin and growth hormone in Pacific salmon are unknown. It was thought that data concerning possible changes in the concentrations of these hormones might provide an indication of their physiological significance.

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Materials and Methods

Collection of Pituitary Glands and Serum

Adult sockeye salmon belonging to the "Chilko race" were collected in 1968 at five locations during their spawning migration. Two samples (groups 1 and 2) were collected at sea approximately 225 and 30 miles, respectively, from the mouth of the Fraser River. Groups 3 and 4 were collected from the Fraser River, 30 and 200 miles, respectively, from its mouth. Group 5 consisted of sexually mature fish captured on the spawning grounds. Sockeye salmon of the same race were also collected in 1969. Group 6 was collected at sea, 30 miles from the mouth of the Fraser River, and groups 7 and 8 were collected from the river, 4 and 30 miles, respectively, from its mouth. Scale samples verified that all fish were from the same race. Table 1 shows numbers in each group, methods of capture, and locations. Immediately after capture, while the fish were alive, 4-ml blood samples were taken from the caudal vein using an evacuated specimen tube fitted to a sterile, disposable, holder-needle unit. Blood was allowed to clot, refrigerated overnight, and centrifuged; the serum was removed with a Pasteur pipette. Merthiolate was added (final concentration, 1:10,000) and the serum was stored frozen. Immediately after the blood was collected, the pituitary glands were removed, frozen in isopentane cooled in liquid nitrogen, and stored.

Preparation of Pituitary Homogenates and Serum Samples

Each pituitary gland from fish of groups 1–5 was homogenized separately in a 13 × 100 mm homogenizer with 4 ml 0.10 M NaCl. The brei was centrifuged, and the supernatant was removed and diluted with 0.10 M NaCl to give three dilutions (1:50, 1:100, and 1:200). Each of these dilutions was assayed separately. In groups 6–8, the same procedure was followed. However, for each of these groups the comparable dilutions were pooled, both those of the pituitary homogenates and those of the sera. These pooled dilutions were then assayed.

Fish size was recorded to determine if any difference in pituitary hormone contents was related to fish size. To determine if any changes in serum hormone concentrations reflected changes in total serum protein concentrations, the latter were measured by the Biuret method (Campbell et al. 1964).

Antiserum Preparations

Antisera to ovine prolactin (NIH-P-S8, 28 IU/mg) and ovine growth hormone (NIH-GH-S9, 1.09 IU/mg) were produced in rabbits. Procedures for immunization and testing the specificity of the sera were described by McKeown and van Overbeeke (1971).

Radioimmunoassay

To prepare tracer antigens, ovine prolactin (NIH-P-S8, 28 IU/mg) and ovine growth hormone (NIH-GH-S9, 1.09 IU/mg) were radioiodinated according to Greenwood et al. (1963). The labelled antigen solutions were diluted to a final concentration equivalent to 100,000 counts/min per 0.6 ml. Radioactivity was measured by a 3 × 3 inch NaI (T1) well crystal, connected to a single channel analyser.

Before the radioimmunoassay was applied, optimum concentrations of antiserum and fish antigen (namely those with which adequate competition between labelled and unlabelled antigen occurred) were determined. The radioimmunoassay used was the solid-phase method of Catt and Tregear (1967), except that the antiserum concentration was higher (diluted only 1:50), commensurate with the relatively high concentrations of fish antigen.

Since neither purified sockeye salmon prolactin nor growth hormone were available, standard curves could not be produced and, therefore, the absolute concentrations could not be determined. However, a serial dilution of a serum sample was used to produce a type of "standard curve" (Fig. 1), and by assigning arbitrary units of

Table 1. Sampling of pituitary glands and serum from sockeye salmon belonging to the "Chilko race."

Group	Approximate location	Date	Miles from the mouth of the Fraser River	Samples: Pituitary glands ♂	Samples: Pituitary glands ♀	Samples: Serum ♂	Samples: Serum ♀	Method of capture
1	Tofino	July 15, 1968	225	2	1	1	1	troller
2	Lummi Island	Aug. 5	30	1	2	5	5	reef net
3	Whonock	Aug. 9	30	2	1	4	4	gillnet
4	Lillooet	Aug. 19	200	1	2	4	4	dipnet
5	Chilko Lake	Sept. 14	375	1	2	5	5	beach sein
6	Lummi Island	July 28, 1969	30	5	5	5	5	reef net
7	Cottonwood	Aug. 1	4	5	5	5	5	gillnet
8	Whonock	Aug. 2	30	5	5	5	5	gillnet

concentration to this curve, relative concentration differences could be determined. The assays for groups 1–5 were conducted separately from those of groups 6–8. Concerning groups 1–5, the samples (both the serum sample and the pituitary homogenate) from one fish from group 1 served as reference samples. The samples for each of groups 6–8 were pooled, and those from group 6 were chosen as a reference. Differences between the various groups of fish were analyzed with Student's *t*-test at a 95% confidence interval.

Results

The pituitary contents of prolactin of sockeye salmon collected in 1968 (groups 1–5) showed an initial decrease, which began while the fish were still in the sea, but was more pronounced during entrance of the fish into the river (Fig. 2). After that, gradual restoration followed. There were no differences in length of the fish between the various groups. The serum concentration of prolactin first increased while the fish were still in sea water, then showed a considerable reduction, after which the level rose again and remained high. No group differences were found in serum protein concentrations.

In 1969, part of the analysis, namely that concerning the entrance into the river, was repeated (groups 6–8, Fig. 2). The pituitary prolactin concentrations in river fish were lower than those in seawater fish. The fish in group 8 were slightly smaller than those in group 7. Serum analysis showed a reduced prolactin concentration in group 8. No differences were found in serum protein concentrations.

The pituitary content of growth hormone in 1968 (groups 1–5) showed no changes during entrance of

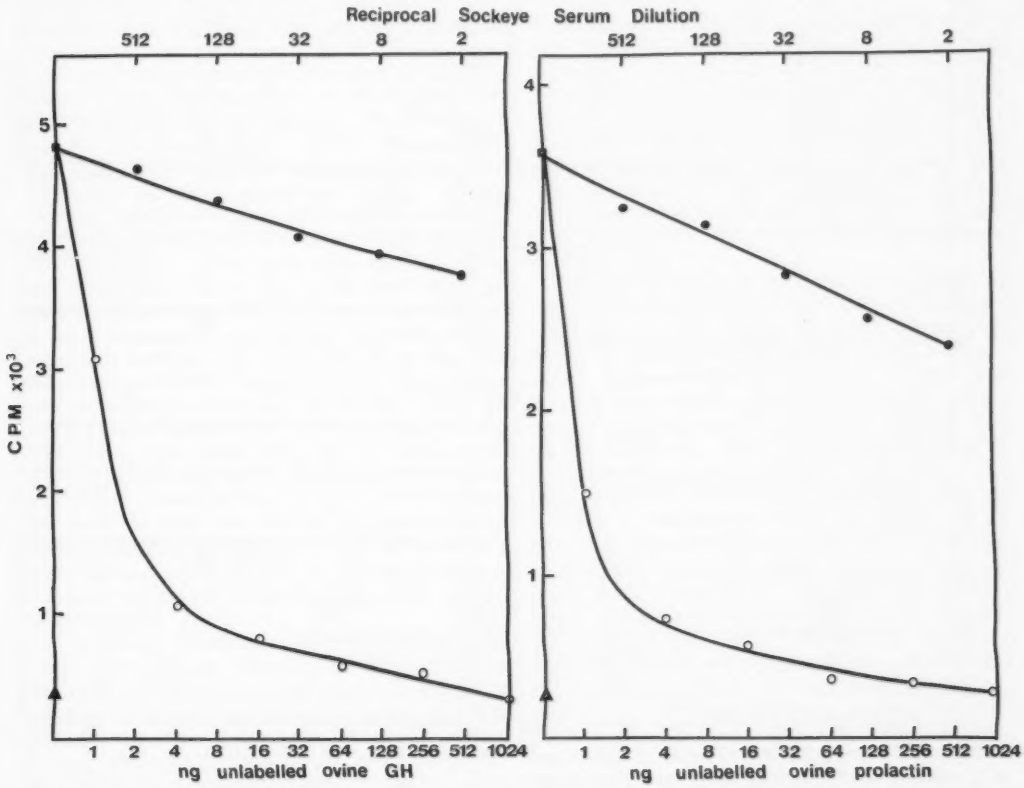

FIG. 1. Standard curve for radioimmunoassay of sockeye salmon serum prolactin and growth hormone. Left: Competitive inhibition of ovine GH-^{131}I to anti-ovine GH by sockeye salmon GH (●) and by ovine GH (○). ■ no unlabelled GH added; ▲ no anti-ovine GH added. Right: Competitive inhibition of ovine prolactin-^{131}I to anti-ovine prolactin by sockeye salmon prolactin (●) and ovine prolactin (○). ■ no unlabelled prolactin added; ▲ no anti-ovine prolactin added.

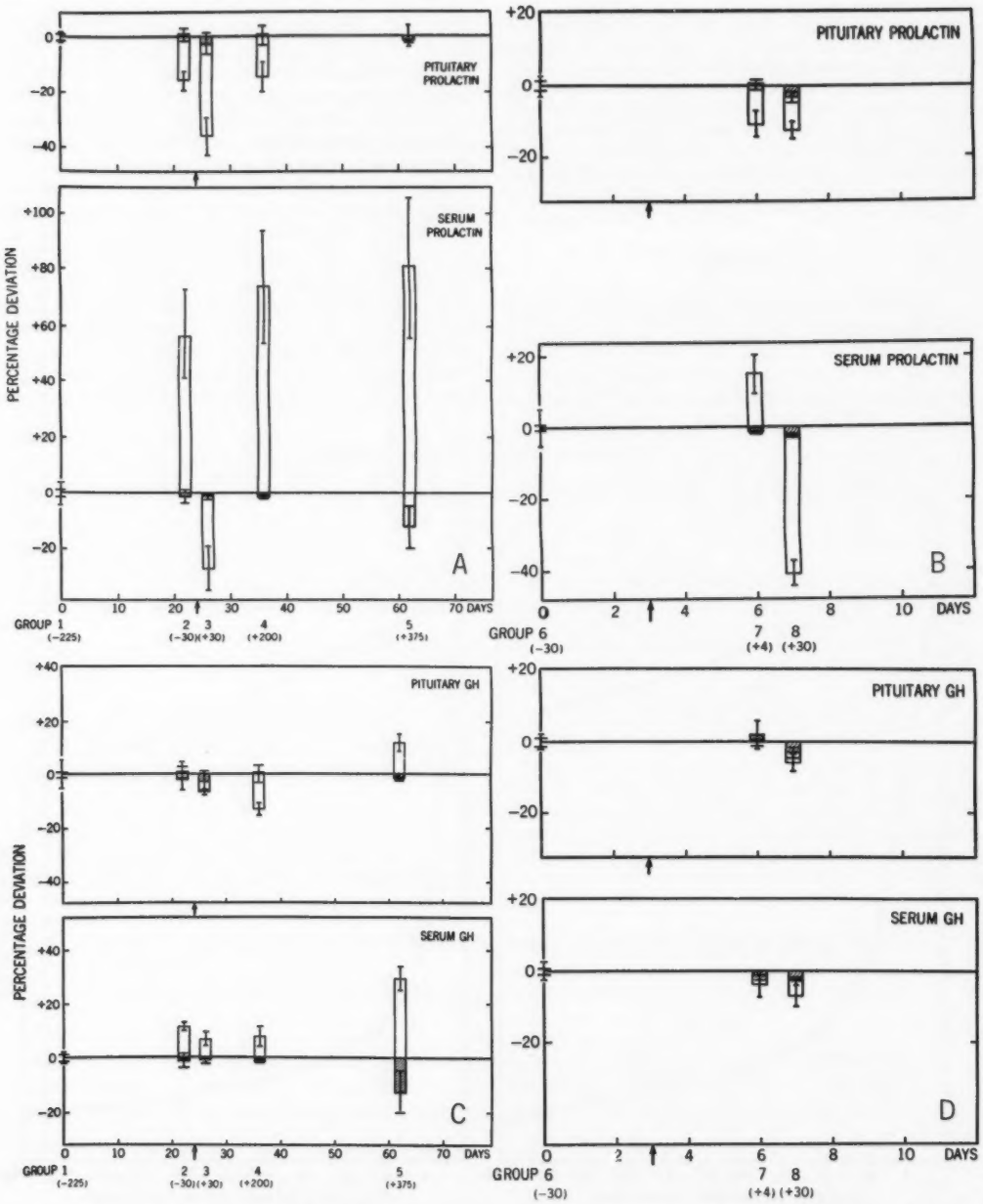

FIG. 2. Changes in pituitary and serum hormone concentrations in adult sockeye salmon, migrating from the ocean to spawning grounds in Chilko Lake, expressed as percentage deviations (±S.E.M.) from concentrations in the first group. Numbers below group numbers indicate distance (*miles*) along migration route between collection sites and the mouth of the Fraser River (−, sites at sea; +, in river). Arrow represents river mouth. Shaded columns represent differences in lengths of fish (upper histograms) and differences in serum protein concentrations (lower histograms). Prolactin concentrations in fish collected in 1968(A) and 1969(B). Growth hormone concentrations in fish collected in 1968(C) and 1969(D).

the fish into the river, but subsequently decreased slightly (Fig. 2). In fish on the spawning grounds, growth hormone concentration had increased. The serum concentration of this hormone first increased when the fish were still in sea water, while the highest level was found in fish on the spawning grounds.

In 1969 (groups 6–8) no differences in growth hormone concentrations in either the pituitary gland or the serum could be found among the three groups (Fig. 2).

Discussion

The concept that prolactin plays an important role in the adaptation of several euryhaline species of teleosts stems from an observation by Pickford and Phillips (1959). They showed that administration of mammalian prolactin prevents the death of hypophysectomized *Fundulus*, when they are transferred from sea water to fresh water. Similar results were obtained in experiments with other species of euryhaline teleosts (Ball and Olivereau 1964; Handin et al. 1964; Schreibman and Kallman 1964, 1966). Support for an osmoregulatory function for prolactin is provided by the fact that the eta cells of the pituitary gland of some euryhaline species exhibit changes indicative of enhanced secretion when the fish, under experimental conditions, are transferred from sea water to fresh water (Ball 1969a, b; Ball and Baker 1969). To our knowledge there exists no direct evidence for a change in prolactin secretion in fish under natural conditions of anadromous migration. A study by Vollrath (1966) concerning the ultrastructure of the eta cells in elver (*Anguilla anguilla*) entering the river suggests, however, that prolactin is indeed involved in the elver's adaptation to fresh water. Our results show that in the sockeye salmon, the most significant change in prolactin concentrations occurred during entrance of the fish into the river. The sharp decrease in the serum prolactin indicates enhanced utilization of the hormone at this time. The accompanying drop in pituitary prolactin indicates that release of the hormone then exceeds its production.

It is difficult to determine the boundary between fresh water and sea water in the Fraser estuary. Moreover, the precise movements of the fish with relation to this boundary are not known. The fact that the reduction in prolactin occurred between Lummi Island, where the fish were in full sea water, and Whonock, where they were in fresh water, strongly suggests that the hormonal change was indeed a response to a drastic change in salinity. Attempts to confirm this conclusion through an analysis of serum prolactin in individual fish, transferred from sea water to fresh water under laboratory conditions, failed because the fish did not survive transportation. The accumulation of prolactin in the serum which preceded the reduction discussed above, is difficult to explain. Possibly, this phenomenon constitutes a form of pre-adaptation or is a response to lower salinities.

Any differences in measured hormone concentrations were probably not due to the methods in which the fish were killed and samples taken, as these were consistent. The method of capture was, however, different in many instances. Fish caught in reef nets, dipnets, or beach seines had similar stresses, but hormonal changes from these samples were often different. Also, fish caught in 1969 by gillnets at two different locations showed variations in serum prolactin levels. Thus, it seems unlikely that the methods of capture had any significant effect on hormone concentrations.

The decreasing pituitary growth hormone contents in adult sockeye during the first part of their migration signifies an increase in release of this hormone relative to its production. The subsequent increase in pituitary growth hormone, apparent in the final stage of the migration, must result from a relatively decreased release. That the serum growth hormone increased throughout the migration may indicate that in fish on the spawning grounds the demand for growth hormone is less than in actively migrating fish.

The significance of a possible mobilization of growth hormone is difficult to assess. Our observations, both in 1968 and 1969, show that it is not a response to the entrance of the fish into fresh water. This is consistent with the observation that growth hormone was unable to promote the survival of hypophysectomized *Fundulus heteroclitus* in fresh water (Burden 1956). The physiological activity of growth hormone in fish is virtually unknown, and the control of its release from the pituitary gland remains to be investigated. In this connection, however, it is of interest that in man, growth hormone is apparently secreted in response to muscular exercise, and this response is mediated by a reduced blood glucose concentration (Hunter and Greenwood 1964; Roth et al. 1964; Hunter et al. 1965). Migratory Pacific salmon also display considerable physical exercise, but this is not accompanied by hypoglycaemia. On the contrary, Robertson et al. (1961) noticed an increased glucose level in migrating chinook salmon (*Oncorhynchus tshawytscha*) which they considered to result from gluconeogenesis. A similar phenomenon in sockeye salmon is indicated by data from Idler and Clemens (1959) showing that during migration there is a drastic depletion of proteins and fats, as well as considerable growth of the liver. Whether this increased metabolic activ-

ity in sockeye salmon involves growth hormone, either directly or through potentiating the effects of other hormones, remains to be investigated.

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Reversible Changes in Adrenal Cortical Cell Morphology and Plasma Hydroxycorticosteroids During Freshwater Portion of the Spawning Journey of Atlantic Salmon (*Salmo salar*)[1]

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HEYL, H. L., AND S. J. CARPENTER. 1972. Reversible changes in adrenal cortical cell morphology and plasma hydroxycorticosteroids during freshwater portion of spawning journey of Atlantic salmon (*Salmo salar*). J. Fish. Res. Bd. Canada 29: 311–314.

Adrenal cortical tissue taken from Atlantic salmon netted in the estuary of the Miramichi River, New Brunswick, at three stages of gonadal activity showed increasing hyperplasia from July to October, with varying degrees of regression or degeneration by the following April. Adrenal cortical cells in April fish contained a characteristic paranuclear dense body, the light and electron microscopic appearances of which are described and discussed. Levels of 17-hydroxycorticosteroids in the plasma almost doubled from July to October and returned to July values by the following April. The presence of these cyclic changes in Atlantic salmon and their absence in Pacific salmon are discussed. Data indicate that genetic factors may be important in determination of the capacity for multiple spawning journeys by some Atlantic salmon.

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Le tissu du cortex surrénalien, prélevé à même des saumons atlantiques capturés au filet dans l'estuaire de la Miramichi (Nouveau-Brunswick) à trois stades de développement des gonades, exhibe une hyperplasie croissante de juillet à octobre, pour atteindre différents degrés de régression et de dégénération en avril de l'année suivante. Chez les poissons capturés en avril, les cellules du cortex surrénalien possèdent un corps paranucléaire dense, dont l'aspect en microscopie optique et électronique est décrit et analysé. Le niveau des 17-hydroxycorticostéroïdes plasmiques double presque de juillet à octobre et retourne à celui de juillet en avril de l'année suivante. L'auteur met en parallèle la présence de ces changements cycliques chez le saumon atlantique et son absence chez le saumon du Pacifique. Les données suggèrent que la capacité que possède le saumon atlantique d'accomplir plusieurs migrations de fraye peut être attribuable à des facteurs génétiques.

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THIS study on Atlantic salmon parallels those done by Robertson and Wexler (1959), and Hane and Robertson (1959), on various species of Pacific salmon. The study was undertaken to clarify certain biological phases in the spawning journey of *Salmo salar* and specifically to follow the course of hyperadrenalcorticism in a species capable of surviving several spawning journeys.

In both Pacific and Atlantic salmon all of the nephros except the rostral portion contains specific renal components (glomeruli, tubules, etc.). Blood vessels of varying size throughout the kidney are often bordered by clumps of small round cells ("hematopoietic tissue"). The T-shaped head end of the kidney, just dorsal to the heart, usually has few distinctly renal elements and consists mainly of small round cells; spotted through this cellular mass are perivascular cuffs or islands of adrenal cortical cells. Changes in these cells between the time the fish enter the river and the time of spawning have been described in both Pacific (Robertson and Wexler 1959; Nandi 1962) and European Atlantic species (Giacommini 1911; Chester Jones 1957). Studies of Atlantic species have used fish collected from water that varied from estuarine to fresh, and have concentrated on fish in early and mature gonadal stages. Our studies of cortical cells in Atlantic salmon were all made on specimens taken from the same estuarine waters, and included fish returning to the ocean after spawning, as well as those in earlier stages described by others. The studies also recorded and correlated the chronological variations in plasma 17-hydroxycortico-

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steroids. Thus, for the first time there is a sequential record of these related changes in Atlantic salmon collected from water of the same salinity at immature, mature, and inactive stages of gonadal development.

Methods

The Atlantic salmon (*Salmo salar*) used were netted at Millbrook, N.B., in tidewater near the mouth of the Miramichi River. The fish were collected in July and October as they started upstream from the ocean, and in April as they descended the river and were about to reenter the ocean. The fact that in addition to the June–July run of sexually immature fish, there is a large October run that enters the Miramichi River from the ocean in a nearly mature gonadal state made it possible to collect specimens of all three stages of sexual maturity in water of the same estuarine salinity. The blood sampling and dissection were carried out at the river's edge within a few minutes of removal from the net. From five to 15 fish were utilized for each stage of gonadal development; both sexes were sampled in each of the three stages.

Blood was obtained by percutaneous heart puncture following the technique of Hane and Robertson (1959). From 25 to 80 cm^3 of blood were usually withdrawn depending on the size of the fish. The heparinized blood was transferred to chilled centrifuge tubes and refrigerated immediately. Within an hour of sampling, the specimens of refrigerated whole blood were centrifuged at high speed for 20 min. The clear, light-colored supernatant plasma (about 60% of the volume of the whole blood) was pipetted into glass bottles and kept in a deep-frozen state until analysis for 17-hydroxycorticosteroids (17–OHCS). Glassware rather than plastic was used throughout the procedure. 17-OHCS analysis was carried out according to the methods of Peterson et al. (1955), and Silber and Porter (1954).

Immediately after blood sampling, the triangular-shaped rostral end of the kidney, which contains the adrenal cortical tissue, was dissected free and placed in Bouin's solution. Following paraffin embedding, the tissues were sectioned serially and stained by routine hematoxylin and eosin procedures.

For electron microscopic study, small pieces ($\sim 1 \times 1$ mm) of rostral kidney from April salmon were fixed for 3–4 hr in ice-chilled, phosphate-buffered, 4% glutaraldehyde (*p*H 7.4, ~ 550 milliosmolal). Following this initial fixation, the tissues were stored in glass vials containing cold, phosphate-buffered 0.45 M sucrose solution until they were brought to the laboratory for final fixation in buffered 1% OsO_4 (Millonig 1962), ethanol dehydration, and embedding in Epon 812. Sections 1–2 μ thick were cut from all blocks of Epon embedded tissue using an LKB Ultratome. These were stained with Paragon 1301 (Spurlock et al. 1965), and examined for adrenal tissue by light microscopy. Thin sections were cut from blocks found to contain adrenal tissue and were mounted on bare 200-mesh copper grids. After staining with uranyl acetate and lead tartrate (Millonig 1961), the thin sections were examined and photographed in a Siemens Elmiskop I electron microscope.

Results

June–July salmon — The gonads in these bright, silvery fish were just starting to enlarge, and were about 4 cm long in an average 3.7-kg (8-lb) fish. Adrenal cortical tissue was already multiplying around blood vessels (Fig. 1A). The large basophilic nuclei of the cells were centrally located in cytoplasm, which was mottled with fine pink granules. Cell membranes were well defined and gave a clean-cut mosaic appearance to the tissue (Fig. 1B).

The plasma 17-hydroxycorticosteroids at this stage averaged 25 µg/100 ml, and were approximately the same in the two sexes (Table 1).

October salmon — These also were bright, silvery fish that had just entered the river from the sea; however, they were heavy with nearly mature egg or milt sacs that filled the body cavity. The individual adrenal cortical cells appeared much as in the June fish, but greatly increased in number. Broad sheets of cells were common (Fig. 2).

The plasma corticosteroids at this stage averaged 42.40 µg/100 ml, the females averaging 46 µg/100 ml, and the males 32 µg/100 ml (Table 1).

April salmon — (black salmon, slinks, or kelts). These fish, netted in the estuary on their way downstream to the ocean, had spawned in the preceding October or November. They were dark-colored; many were thin and sluggish, but a few seemed plump and lively. The adrenal cortical cells showed much the same degree of proliferation as those in the October specimens. Large masses of cells were still common. In many areas, however, the cell arrangement was less compact, and the area of cortical cells was being invaded by blood vessels, connective tissue, and small round cells (Fig. 3A). Most fish showed varying degrees of cellular deterioration, including vacuolization of nuclei, swelling and disruption of cytoplasm, and a consequent loss of the neat mosaic architecture of the tissue (Fig. 3B). However, there was great variation from fish to fish, and of the sixteen fish examined, four had cortical cells (Figs. 3C and 3D) that closely resembled those seen in the bright June fish.

The plasma corticosteroids at this stage averaged 23.9 µg/100 ml (Table 1).

Many cortical cells in these salmon contained a cytoplasmic structure resembling an inclusion body (Fig. 4). This usually was seen midway between the peripherally placed nucleus and the central cell border; it was often twice the size of the nucleolus and

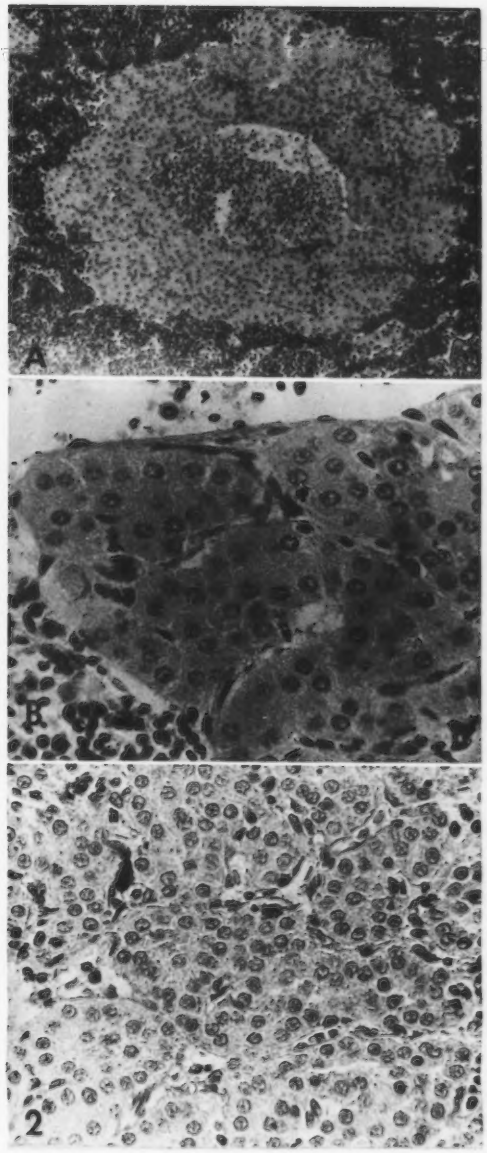

FIG. 1. (*Top and center*) Adrenal cortical cells beginning to proliferate as a narrow cuff around a blood vessel in June–July fish. Hematoxylin and eosin stain. (A), Hematopoietic tissue (periphery) fills the space between blood vessels. × 158. Under higher magnification (B), note the characteristic large centrally placed basophilic staining nuclei, the finely granular eosinophilic cytoplasm and the mosaic appearance created by cell membranes. × 630.

FIG. 2. (*Bottom*) Sheet of adrenal cortical cells in advanced stage of proliferation typical of October fish. *H & E stain* × *504.*

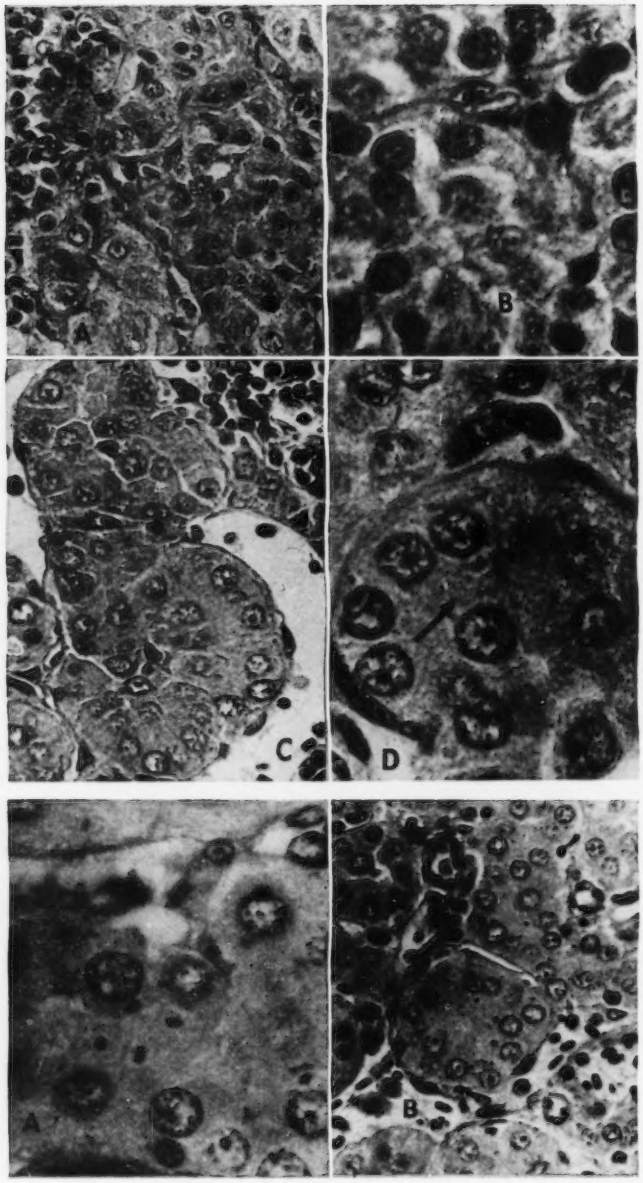

FIG. 3. Adrenal cortical cells in April fish (H & E stain) showing (A) variation in size and shape (× 600), and (B) swelling of cell bodies and disruption of the mosaic appearance (× 1500). Some April salmon had cortical cells relatively unchanged from those typical of June fish: (C) (× 600) and (D) (× 1500). Compare 3A and B with 3C and D.

FIG. 4. (A) Cluster of paranuclear dense bodies typical of April fish; note barrel and hourglass shapes, halos, and consistent position in cytoplasm (H & E stain × 1500) (see also Fig. 3D, arrow). (B) Glandular arrangement of adrenal cortical cells, showing paranuclear "dense bodies" forming an inner concentric ring. H & E stain × 600.

FIG. 5. (*Top*) Electron micrograph of portion of adrenal cortical cell (April salmon) showing details of a paranuclear dense body (DB) and mitochondria (M). Note faint filamentous pattern of matrix of dense body and tubular cristae of the mitochondria. ER, endoplasmic reticulum; N, nucleus; R, free ribosomes. × 20,405.

FIG. 6. (Bottom) Electron micrograph of adrenal cortical cell cytoplasm showing mitochondria with internal deposits of dense, osmiophilic material (arrows). F, bundle of microfilaments. × 9540.

TABLE 1. Plasma 17-hydroxycorticosteroids (μg/100 ml) in three gonadal stages of Atlantic salmon netted in estuarine water.

Sex and weight	July (immature)		Oct. (mature)		Apr. (inactive)	
	No. of fish	Avg (range)	No. of fish	Avg (range)	No. of fish	Avg (range)
			Male			
Grilse (4–5 lb)	3	27.0 (21.6–30.0)	0	–	0	–
Salmon (7–10 lb)	0	–	4	33.1 (27.8–39.8)	2	27.0 (23.3–30.7)
			Female			
Grilse (4–5 lb)	3	28.4 (22.1–33.9)	0	–	0	–
Salmon (7–10 lb)	2	19.3 (14.6–24.0)	8	47.0 (24.3–58.5)	3	22.8 (16.2–28.2)
All specimens	8	25.5 (14.6–33.9)	12	42.4 (24.3–58.5)	5	23.9 (21.1–30.7)

in a different focal plane. It stained a homogeneous hyalinelike pink with hematoxylin and eosin; most of these structures had a clear border, or halo, setting it off from cytoplasm. Hourglass and barrel shapes were common. Where cortical cells were arranged in tubular or glandular clumps the nuclei of adjacent cells formed an outer circle and the "inclusion bodies" an inner concentric one. In electron micrographs (Fig. 5) these structures were seen as membrane-limited, vesicular dense bodies with a diameter range of 2.0–4.0 μ; occasionally, there was more than one per cell. At lower magnifications (Fig. 6) the contents of these bodies seemed amorphous, uniformly osmiophilic, and generally similar in appearance to deposits of dense material occasionally found within mitochondria. At higher magnifications, however, a faint filamentous substructure was apparent (Fig. 5). No spaces that might conform to the "halos" observed by light microscopy were seen about the circumference of the bodies.

Discussion

Cyclic Changes — This first report of adrenal and hydroxycorticosteroid changes during the 10–11 month river portion of the spawning journey of Atlantic salmon emphasizes an important difference from the Pacific species, namely the capacity of the Atlantic salmon for cyclic change. The level of plasma hydroxycorticosteroids in the immature June fish (25.5 μg/100 ml) was comparable to that recorded by others for both Atlantic (Fontaine and Leloup-Hatey 1954) and Pacific (Hane and Robertson 1959) species at the same stage. However, although proliferation of adrenal cortical tissue in October Atlantic salmon was considerably greater than that noted in the June specimens, the difference was not as striking as that described in Pacific fish; it was rare, for instance, that cortical tissue could be easily spotted in gross cross sections of the rostral end of the nephros as described by Robertson and Wexler (1959). Moreover, the average concentration of plasma hydroxycorticosteroids in October Atlantic salmon (42 μg/100 ml) was considerably less than that found in Pacific salmon of comparable sexual maturity (60–100 μg/100 ml). This difference reflects the stabilization of plasma corticosteroid values in Atlantic salmon at a gonadal stage when values in Pacific species are still rising. By April, as the Atlantic salmon reentered the ocean, the plasma corticosteroids had returned to the June values, thus completing a cyclic rise and fall not seen in Pacific salmon.

Thus, this cyclic phenomenon is characteristic of *Salmo salar*, a species capable of repeated spawning journeys. In Pacific salmon, which usually die after the initial spawning effort, there is no regression. Idler and Truscott (1963) have demonstrated that Atlantic salmon can metabolize cortisone more effectively than Pacific salmon. Their biochemical evidence may partially explain our observations of reversible and cyclic changes. Robertson et al. (1961) emphasized the similarity between human hyperadrenocorticism (Cushing syndrome) and the adrenal cortical cell proliferation in Pacific salmon nearing gonadal maturity. Our studies indicate that *Salmo salar* is capable of reversing the pituitary governed process of adrenal cortical cell proliferation, which in man is manifested by an irreversible disease.

Genetic Factors — This study indicates that individual genetic characteristics may be determinants in the multiple spawning journeys of some Atlantic salmon. In New Brunswick, the spring sport fishing for black salmon is popular, while in Quebec and Scotland comparable fish are scorned as "slinks" or "kelts." Within the species *Salmo salar* there may be individual fish carrying a genetic factor that allows them to metabolize cortisone better than others. The fact that some New Brunswick black salmon had cortical cells showing no evidence of deterioration indicates the possibility that these were the individual fish most likely to survive the spawning journey and return another year. These may also be the rare black salmon that fight well on rod and reel.

This individual variation is comparable to that noted in the corpuscles of Stannius of black salmon (Heyl 1970); although corpuscle cells from many April fish showed degenerative changes, there were striking individual exceptions in which cells showed the same clearly defined nuclei and heavily granular cytoplasm characteristic of specimens from June fish.

Paranuclear Dense Bodies — The unusual cytoplasmic dense bodies frequently seen in adrenal cortical cells from April specimens were also seen, although much less commonly, in October fish. A few were even found after a careful search in June specimens. Their consistent paranuclear location and variation in size make the possibility of a parasite unlikely. The hyalinelike appearance of the hourglass or barrel-like shapes in hemotoxylin–eosin preparation under light microscopy were not unlike inclusion bodies but their variation in size, precise location, and usual restriction of one to a cell were inconsistent with this interpretation.

Electron microscope studies by Yamamoto and Onozato (1965) and Ogawa (1969) noted the presence of occasional, membrane-enclosed, dense, osmiophilic bodies in the adrenal cortical cells of the goldfish. It is doubtful that these were the same structures found in *Salmo salar*. Neither of these authors observed the filamentous substructure we have de-

scribed in the matrix of the granules. Moreover, in goldfish these dense bodies rarely exceeded 1.0 μ in diameter while those in *Salmo salar* ranged from 2 to 4 μ. Finally, their location within the cytoplasm varied in goldfish but was constant in Atlantic salmon.

Pending further investigation, the origin, chemical composition, and functional significance of the dense bodies must remain matters for conjecture. There is no evidence at present that they arise as part of the lysosome system. On the other hand, the possibility that they may represent transformed mitochondria is indicated by the presence of osmiophilic material in some of the latter organelles. Giacomelli et al. (1965) postulated that similar deposits seen in the mitochondria of mammalian adrenal cortical cells represented intermediates in steroid biosynthesis. If conversion of mitochondria to dense bodies does occur in the adrenal cortical cells of the Atlantic salmon, it would be reasonable to assume that the dense material within the bodies also is composed of stored steroid intermediates. The observed fall in plasma hydroxycorticosteroid levels noted at this stage of the Atlantic salmon life-cycle may be related to an increased storage of steroid hormones or intermediates within the adrenal cells.

Acknowledgments

The investigators wish to acknowledge the valuable assistance of Mr E. Schofield of the Fisheries Research Board of Canada and his staff at Millbank, N.B.; Dr E. Block and Dr E. Paulsen of the Albert Einstein School of Medicine in New York; Dr K. Benirschke and Dr E. Harris at the Dartmouth Medical School; and K. Heyl and S. Atherton.

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Effects of Four Insecticides on the Ability of Atlantic Salmon Parr (*Salmo salar*) to Learn and Retain a Simple Conditioned Response

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HATFIELD, C. T., AND P. H. JOHANSEN. 1972. Effects of four insecticides on the ability of Atlantic salmon parr (*Salmo salar*) to learn and retain a simple conditioned response. J. Fish. Res. Bd. Canada 29: 315–321.

The learning ability of untreated, acetone-treated, and insecticide-treated Atlantic salmon parr was determined in a shuttlebox conditioning apparatus. Learning improvement on second conditioning was also tested.

The results were that: (1), acetone did not affect learning; (2), with treatment for 24 hr at the 96-hr LC50 Sumithion® completely inhibited learning, Abate® retarded learning, DDT mildly enhanced learning, and methoxychlor was without a detectable effect; (3), when Abate and methoxychlor-treated salmon in item (2) above were retrained 1 or 7 days later their learning ability improved; but DDT-treated fish showed no improvement; (4), four days of recovery from a 24 -hr exposure to the 96-hr LC50 of Abate or Sumithion still resulted in slow learning ability, although after 7 days of recovery learning rate was the same as that of controls; (5), insecticide treatment at the 96-hr LC50 level for 24 hr interposed between first and second conditioning had little or no effect on learning ability; (6), insecticide concentrations at one-tenth the 96-hr LC50 or lower had no effect on learning ability.

HATFIELD, C. T., AND P. H. JOHANSEN. 1972. Effects of four insecticides on the ability of Atlantic salmon parr (*Salmo salar*) to learn and retain a simple conditioned response. J. Fish. Res. Bd. Canada 29: 315–321.

Les auteurs ont mesuré l'aptitude à l'apprentissage de tacons de saumon atlantique non traités, traités à l'acétone et enfin traités aux insecticides. Ils ont également évalué les progrès de l'apprentissage après deuxième conditionnement.

Ils ont obtenu les résultats suivants: (1) l'acétone n'affecte pas l'apprentissage; (2) avec un traitement de 24 h au LC 50–96 h, le Sumithion® bloque complètement l'apprentissage, l'Abate® le retarde, le DDT le facilite un peu et le méthoxychlor n'a pas d'effet visible; (3) lorsque les saumons traités à l'Abate et au méthoxychlor comme en (2) sont soumis à un réapprentissage 1 à 7 jours plus tard, leur aptitude à apprendre est améliorée; par contre, les poissons traités au DDT ne démontrent aucune amélioration; (4) une période de récupération de quatre jours après exposition de 24 h au LC 50–96 h de l'Abate et du Sumithion n'accélère pas l'apprentissage qui demeure lent, bien qu'après 7 jours de récupération, la vitesse d'apprentissage soit la même que celle des témoins; (5) un traitement aux insecticides au niveau du LC 50–96 h pendant 24 h, interposé entre le premier et le second conditionnement, n'a que très peu ou pas d'effet sur l'aptitude à l'apprentissage; (6) des teneurs en insecticides d'un dixième ou moins de celles du LC 50–96 h n'ont pas d'effet sur l'aptitude à l'apprentissage.

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A number of studies have shown that insecticides can alter various aspects of an animal's behaviour (Mount 1962; McEwan and Brown 1966) as well as an animal's learning capabilities (Anderson and Peterson 1969; Anderson and Prins 1970). Since many of the latter studies have been restricted to a single insecticide, a study comparing the effects of several insecticides upon learning ability seemed warranted. This report contains the results of such a study in which four insecticides (DDT, methoxychlor, Sumithion®, and Abate®) were used at their 96-hr LC50 and at $\frac{1}{10}$ of this concentration or the recommended field application level to treat salmon parr at various stages of the training cycle.

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Materials and Methods

Holding Facilities

Facilities are fully described in Hatfield (1970). In summary, the salmon (*Salmo salar* L.), 10–15 cm long, were acclimated to 15 ± 1 C for 2 weeks before use in circulating soft water (*p*H 6.8–7.1; total hardness 14.0 ± 2.0 ppm as $CaCO_3$). The fish were fed twice daily on a commercial trout chow which was insecticide free (V. Zitko personal communication) and kept on a photoperiod cycle of 8 hr daylight and 16 hr darkness.

Fish Treatment

Sprague (1969) and others state that, during bioassay tests with fish, a minimum ratio of 1 litre of treatment solution per g of fish should be maintained. Individual fish were therefore treated in polyethylene-lined, fibreglass tanks containing 25 liters of static, aerated water. Each exposure was for 24 hr at 15 C. The fish were then transferred to 25 liters of untreated water for 24 hr before being placed in the conditioning apparatus. This procedure was adopted to reduce contamination of the training apparatus and allow fish to recover somewhat from acute effects of the treatment.

DDT (1, 1, 1-trichloro-2,2-bis (*p*-chlorophenyl) ethane (*p,p'* isomer 99 + %) and methoxychlor (1,1,1-trichloro-2,2-bis (*p*-methoxy phenyl) ethane 89.5% (technical grade) were obtained from City Chemical Corporation, New York. For fish treatment DDT and methoxychlor were first dissolved in acetone and the solution then added to the water.

Sumithion (0,0-dimethyl 0-(4-nitro-*m*-tolyl) phosphorothioate 55%) and Abate 4-E (0,0,0′,0′-tetramethyl 0,0′-thiode-*p*-phenylene phosphorothioate 80%), supplied by Cyanamid of Canada Ltd., were added as solutions in water.

The Sumithion was fractionated by column chromatography on silica gel and analysed by thin-layer chromatography on silica gel by Dr V. Zitko, Fisheries Research Board of Canada, St. Andrews. Infrared spectroscopy was used as a check. The sample contained 55% Sumithion, Sumioxon, 3-methyl-4-nitrocresol and another nitrophenol, 15% volatile solvent (mainly xylene), 10% surfactant (a polyethylene glycol ether), and 4% Sumithion and surfactant. Sixteen percent was lost in separation.

The Abate 4-E formulation was made up of 80% Abate, two solvents (mainly Fanasol AN-3 with some Emcol H-140), and an emulsifier (Aerosol OT) (Cyanamid of Canada Ltd. personal communication). We did not study the effects on learning of the component parts of either the Sumithion or the Abate mixtures. Thus, in this study Sumithion and Abate refer to the entire formulation supplied to us.

Untreated and acetone-treated control fish were handled in the same manner as insecticide-treated ones except that no insecticide was dissolved in the acetone or treatment water. Acetone-treated fish were exposed to the same quantity of acetone as was used to carry the desired amounts of the organochlorine insecticides into the insecticide containing water.

Conditioning Apparatus

The conditioning shuttlebox was identical to that used by Jackson et al. (1970) except that a 40-watt incandescent bulb was used as the light source in each chamber. Water circulated through the shuttlebox at 1 liter per min and was maintained at a constant depth of 16 cm. Water temperature was the same as that for acclimation and treatment.

Conditioning Procedure

Light served as the conditioned stimulus (CS) and an electric shock as the unconditioned stimulus (UCS). The training procedure was similar to that used by Roots and Prosser (1962).

Conditioning trials were run in a dark room and every effort was made to avoid vibrations in the apparatus during tests. Tests were run between 1100 and 1400 hr. The final training procedure was as follows: (1) A single fish was placed in the shuttlebox. Lights were left on in both chambers but turned off in the room and the fish left undisturbed for 5 min; (2) The light was turned off in one chamber and a series of five trials was carried out during which the lighting was switched every minute so that one chamber became light while the other became dark. Any initial lighting preference of the fish was indicated when it swam into the appropriate chamber after each lighting switch; (3) Fish preferring the light chamber (in practice less than 1 in 20) were rejected because we felt that the door could be seen more easily by a fish in the dark chamber than one in the light chamber and thus the light-preferring fish would be at a disadvantage when conditioning was attempted. Conditioning proceeded for fish having no preference or a preference for the dark chamber; (4) The lighting was switched so the fish was in the dark chamber; (5) Fifteen sec were allowed to elapse; (6) A continuous shock of 20.0 mv-sec duration, 400 C/S square-wave pulses was administered for 45 sec or until the fish escaped through the door into the lighted chamber (usually within 5–10 sec). Voltage was varied within a 20–30 v range to produce moderate activity in the fish; (7) The response of the fish was recorded as a "miss" (M) if it did not leave the chamber during the shock period, a "searching escape" (SE) if it left during the period but did not go immediately through the door when shocked, a "direct escape" (DE) if it passed directly through the door when first shocked, and an "avoidance" (A) if it succeeded in avoiding the shock altogether by moving through the door during the 15-sec interval after the lighting was switched; (8) If the fish elicited an (M) the lighting was switched immediately after the shock to place the fish in a lighted chamber; (9) An intertrial interval (ITI) of from 1-2 min (depending on response time in steps 5 or 6) was allowed during which time the UCS was maintained in the dark chamber to discourage random swimming of the fish through the chamber door; (10) Steps 4–9 were repeated until: (a) eight consecutive avoidances were elicited by the fish, whereupon it was assumed to be conditioned, or (b) eight consecutive misses were elicited by the fish, whereupon it was assumed to be incapable of learning,

or (c) seventy-five trials were conducted with the fish without either the a) or b) criterion being met, whereupon the fish was assumed to be incapable of learning. The criterion number of (A) or (M) in parts (a) or (b) of step 10 were not included when the total number of trials to condition a salmon was recorded.

Except for learning improvement experiments, where fish were tested twice before being destroyed, individual salmon were only tested once for conditioning, then destroyed.

Learning improvement was calculated as follows:

$$\text{Improvement} = 100\% - \left(\frac{\text{trials to criterion, 2nd training period}}{\text{trials to criterion, 1st training period}} \right) \times 100$$

All conditioning was done from October 8, 1969, to March 15, 1970. Subjects for experimentation with any one insecticide were taken from the same lot of fish. They were selected randomly and controls were run in alternation with experimental fish when practical, otherwise they were run within the same week. With the exception of learning improvement results, for which no statistical analysis was used, all data were analysed using the Mann-Whitney U test, $p = 0.05$.

Experimental Procedures

The detailed methods for each of the experimental situations are outlined with the results of those experiments.

Results

From preliminary experiments we determined that the conditioned response was learned most rapidly between 1100–1400 hr, that the length of the intertrial interval (ITI) (whether 1, 2, or 3 min) did not influence conditioning and that no difference in conditioning was caused by continuous or intermittent electric shock. Therefore, all experiments were done between 1100–1400 hr with an ITI of 2 min and with continuous electric shock.

Other experiments showed no statistically significant effect of acetone on conditioning.

Preliminary experiments showed that improvement was consistently high after 1 or 2 days had elapsed between the first and second conditioning. Longer periods of up to 2 weeks resulted in lower levels of improvement.

Experiment 1. Parr Treated Near Their 96-hr LC50

The purpose of this experiment was to determine whether the treatment of salmon with insecticides at a concentration near their 96-hr LC50 would affect initial learning ability. Fish were treated individually with DDT, methoxychlor, Abate, or Sumithion for 24 hr at a concentration near the 96-hr LC50 for salmon. This was about 1.0 ppm for Sumithion (J. B. Sprague personal communication), 0.07 ppm for DDT (Gagnon 1958), 0.09 ppm for methoxychlor and 5.0 ppm for Abate (personal bioassay tests). Ten fish were treated with each insecticide. Conditioning tests were run after fish were held in untreated water for 24 hr.

Fish treated with 1.0 ppm Sumithion for 24 hr had their learning ability completely inhibited. They appeared less active than control fish and reacted slowly to external stimuli, but otherwise seemed normal. Treated fish were active for the first 20–30 trials in every conditioning attempt but exhibited more "miss" responses than control fish.

Abate at 5.0 ppm significantly interfered with the learning process although most treated fish did learn the response (Fig. 1a). Treated salmon were less active than normal and more "miss" responses were recorded than for controls.

Salmon treated with 0.07 ppm DDT learned significantly faster than controls (Fig. 1b). The fish appeared hypersensitive to any external stimuli when in the apparatus. Many "misses" were recorded but most responses were either "direct escapes" or "avoidances".

Treatment with 0.09 ppm methoxychlor had no significant effect on learning speed (Fig. 1c) and the learning patterns of control and methoxychlor treated fish were similar.

Experiment 2. Parr Treated at Field Concentrations or One-tenth the 96-hr LC50

This experiment was designed to show any effects on learning of organophosphates at concentrations found in water after field applications or of organochlorines at one-tenth the 96-hr LC50. Six fish were tested for each treatment. Sumithion and Abate were used at a concentration recommended by the insecticide manufacturers or applicators for insect control. This was approximately 0.1 ppm for an aerial application of Sumithion (Interdepartmental Committee on Forest Spraying Ottawa) and 0.1 ppm for a ground application of Abate (Anon. Cyanamid of Canada Ltd. 1964). For the organochlorine insecticides, the recommended ground application level of 0.1 ppm insecticide in water, which is usually given over very short time periods, (Hocking et al. 1949; A. S. West personal communication) is well above the 96-hr LC50 of salmon. Therefore, for both DDT and methoxychlor, a concentration one-tenth the 96-hr LC50 was used (0.007 ppm DDT and 0.009 ppm methoxychlor). Conditioning tests were run after the fish had been in untreated water for 24 hr.

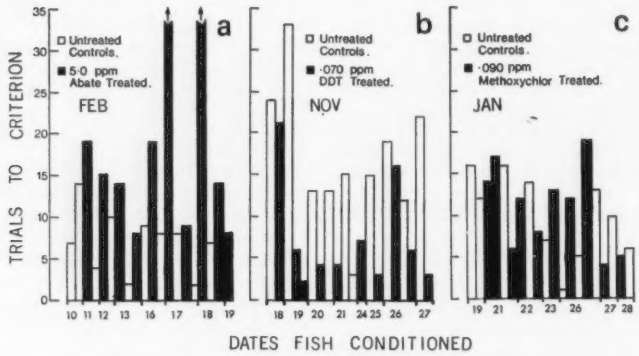

FIG. 1. Experiment 1, Learning ability of fish after treatment for 24hr in (a), 5.0 ppm Abate; (b), 0.07 ppm DDT; and (c), 0.09 ppm methoxychlor. Each bar represents one fish. Arrows indicate >75 trials without conditioning.

Sumithion at the 0.1 ppm level did not significantly affect learning speed of salmon (Fig. 2a). A larger than normal number of "miss" responses were recorded however. No significant effect on learning speed was found for the fish treated with 0.1 ppm Abate (Fig. 2b). The learning ability of fish treated with 0.007 ppm DDT or 0.009 ppm methoxychlor was not altered significantly (Fig. 2c, 2d).

EXPERIMENT 3. PARR TREATED AT 96-HR LC50 FOR 24 HR TRAINED THEN RETRAINED

Effects of the insecticides on learning improvement were measured in this experiment. Fish, which could still learn after treatment with one of the four insecticides at the concentrations used in Experiment 1 (96-hr LC50), were retested in the conditioning apparatus after 1 or 7 days. Six fish were used at each time and per cent improvement in learning was calculated.

No 1.0 ppm Sumithion-treated fish could be tested since these fish were not conditioned in Experiment 1. However, fish treated with 5.0 ppm Abate then conditioned showed improvement in learning speed when retested both 1 day (Fig. 3a) after the initial training and 7 days (Fig. 3b) after the initial training period. There was no difference between the improvement in learning speed of these fish and the improvement of untreated control fish tested after the same periods of time had elapsed.

Fish treated with 0.07 ppm DDT, conditioned, and then retested 1 or 7 days later, showed scattered improvement (Fig. 3). Three fish improved their scores after 1 day but only one after 7 days. All fish were eventually conditioned during the second session.

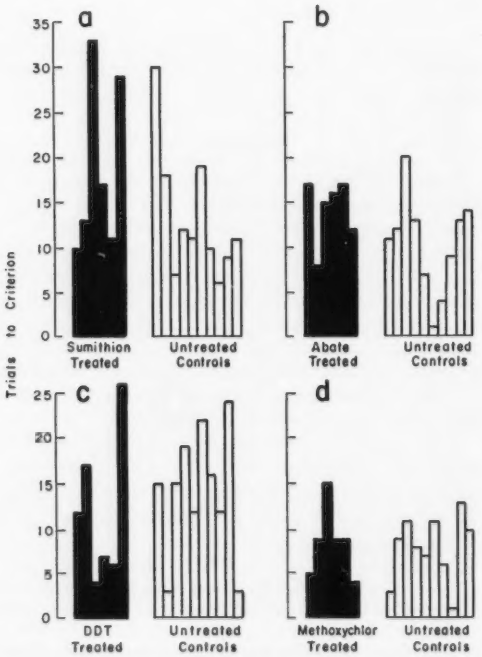

FIG. 2. Experiment 2, Learning ability of fish after treatment for 24 hr in (a), 0.1 ppm Sumithion; (b), 0.1 ppm Abate; (c), 0.007 ppm DDT; or (d), 0.009 ppm methoxychlor. Each bar represents one fish.

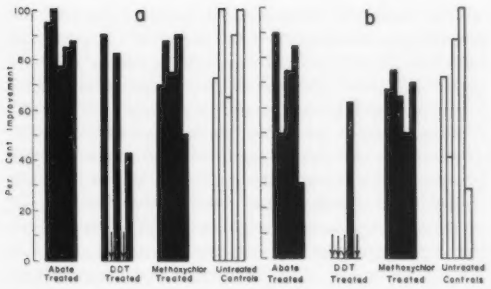

FIG. 3. Experiment 3, Learning improvement in fish retested in the conditioning apparatus (a), 1 day (b), 7 days after the first conditioning session in experiment 1. Each bar represents one fish. Arrows indicate no improvement in learning.

Methoxychlor-treated fish showed improvements in learning similar to the controls for both the 1 and 7 day intertraining period (Fig. 3).

EXPERIMENT 4. PARR TREATED AT 96-HR LC50 FOR 24 HR LEFT IN UNTREATED WATER THEN TRAINED

This experiment was designed to measure the duration of the effects on learning caused by the insecticides. Fish were treated for 24 hr at the 96-hr LC50 of an insecticide, transferred to untreated water and tested in the conditioning apparatus after a 4 or 7 day recovery period. Six fish were tested at each time. The experiment was terminated if the fish returned to the learning rate of control fish after the 4 day recovery period.

The learning speed of fish treated with 1.0 ppm Sumithion then left in untreated water for 4 days was slower than controls. However, after 7 days recovery the fish learned at a rate similar to control fish (Fig. 4a). Fish treated with 5.0 ppm Abate also did not learn normally after 4 days recovery but fish allowed to recover 7 days learned at a rate similar to controls (Fig. 4b). After 4 days recovery following treatment with 0.07 ppm DDT or 0.09 ppm methoxychlor, fish were conditioned at the control fish rate (Fig. 4c, 4d).

EXPERIMENT 5. PARR TRAINED, TREATED 24-HR AT THE 96-HR LC50 THEN RETRAINED

This experiment was designed to determine the effects on second conditioning (learning improvement) of an insecticide treatment at the 96-hr LC50 interposed between first and second conditioning. Five naive, untreated fish were conditioned, immediately exposed for 24 hr to one of the four insecticides at the 96-hr LC50 values used

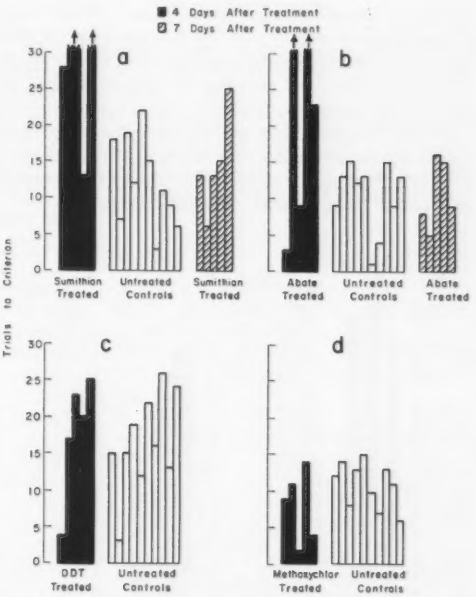

FIG. 4. Experiment 4, Fish conditioned 4 or 7 days after a 24-hr treatment in (a), 1.0 ppm Sumithion; (b), 5.0 ppm Abate; (c), 0.07 ppm DDT; or (d), 0.09 ppm methoxychlor. Each bar represents one fish. Arrows indicate >75 trials without conditioning. (No DDT or methoxychlor-treated fish were trained after 7 days, since learning ability already appeared normal in fish treated and tested after 4 days).

in Experiment 1, left in untreated water for 24-hr, then reconditioned.

Learning improvement in some fish was affected by the Sumithion treatment (Fig. 5a), while learning in other fish did not seem affected; all fish were eventually conditioned. This is in contrast to results from Experiment 1 where fish not previously taught could not be conditioned after treatment with 1.0 ppm Sumithion. Abate at the 5.0 ppm level had a similar effect on learning improvement as Sumithion (Fig. 5b) in that some fish were affected by the chemical while others apparently were not. All fish were eventually conditioned. In contrast to this, DDT and methoxychlor appeared to have little or no effect on learning improvement at the 0.07 ppm and 0.09 ppm treatment levels respectively (Fig. 5c, 5d).

Discussion

The finding of this study that learning in salmon can be retarded by organophosphates or enhanced

by some organochlorine insecticides (DDT) supports similar results found by Warner et al. (1966) with goldfish. Why methoxychlor did not show an enhancing effect on learning of salmon similar to DDT, is uncertain. Possibly the chemical was metabolized or eliminated from the fish faster than DDT, or the unusually fast learning ability of both the methoxychlor-control and methoxychlor-treated fish could have masked any differences.

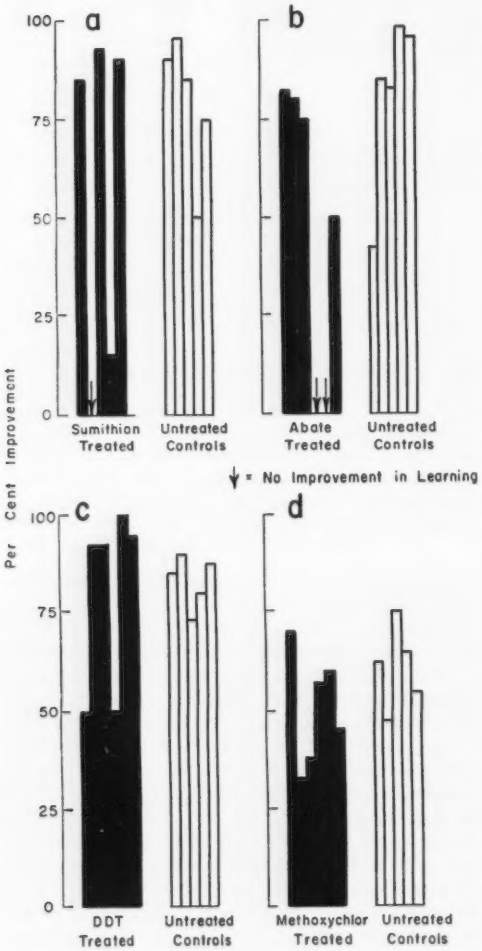

FIG. 5. Experiment 5, Per cent improvement in learning of fish conditioned, treated in (a), 1.0 ppm Sumithion; (b), 5.0 ppm Abate; (c), 0.07 ppm DDT or (d), 0.09 ppm methoxychlor, then retested a second time in the conditioning apparatus. Each bar represents one fish.

The variable improvement in learning on the second conditioning of 0.07 ppm DDT-treated fish was interesting since all fish treated with any of the other chemicals showed large improvements. This variable improvement could be a result of the fish having learned at their fastest attainable rate. However, if the data from fast learning control fish are pooled, it is evident that the scores of all these individuals improved on second conditioning. It, therefore, appears that these DDT-treated fish did not retain the associations learned in the first conditioning and that their enhanced learning rate was temporary and artificial. This was further established by the results of Experiment 4, in which it was found that fish left in untreated water for 4 days after a DDT treatment learned at the same rate as untreated fish.

Dawson and McGaugh (1969) found that an electroconvulsive shock given to rats immediately after they were conditioned interrupted their memory consolidation process and as a consequence reduced retention ability for the learned response. This finding in rats may be related to the trained-treated-retrained experiment with salmon where we found that the organophosphates reduced learning improvement on second conditioning which might be an indicator for lowered retention ability of a learned response. It should be noted, however, that all fish could be conditioned. In contrast to this it was found that in the treatment-trained situation learning was markedly retarded (Abate) if not completely inhibited (Sumithion). This indicates that initial learning capacity, more than retention ability, is affected by these insecticides.

It was apparent that activity played a large role in all our experiments on learning. A case could be made that variation in this one parameter between differently treated groups of fish accounted for the different rates of learning measured. There is no doubt that activity is important in learning, especially in a shuttlebox such as used.

However, it is doubtful if a general change in basic activity levels of fish after different treatments could account for the varying learning ability results. Hyperactive 0.07 ppm DDT-treated fish did not stray into the wrong chamber between trials more often than control fish. Less active 1.0 ppm Sumithion-treated fish frequently made the correct associations between light and safety but were not successful in stringing them together into a consistent normal pattern. It is difficult to see, therefore, how a change in activity alone could explain the enhanced or inhibited learning in these fish.

Although salmon treated with the high doses of the organophosphates exhibited a greater number

of "misses" than untreated control fish, this did not seem to account for the inhibited or retarded learning. A larger than normal number of "misses" were also recorded for fish treated with 0.07 ppm DDT-, 0.1 ppm Sumithion-, and 0.1 ppm Abate. If the number of these responses alone were the indication of how learning speed was affected by these chemicals, one would expect all groups of treated fish which have large numbers of "miss" responses in their learning pattern to be slow learners. The data in this study do not support this postulation.

Our results indicate that the lower concentrations of the 4 insecticides used in this study have no detectable effect upon learning speed. This would seem to support the suggestion that in some instances one tenth the 96-hr LC50 may be a "biological safe" level for a pollutant in the environment (Mount and Stephan 1969; Sprague 1970). However, our support for this suggestion is conditional since in our study the levels of insecticide actually present in the water and therefore available to the fish may have been considerably lower than the added amounts as a result of adsorption and/or absorption on to the plastic liner of the exposure tanks. It is obvious that future studies must rely upon chemical determinations of the insecticide levels actually present in the water.

As was mentioned earlier, the levels of the organochlorine insecticides used for aquatic insect control are above the reported 96-hr LC50. We found that a 24 hr exposure to the 96-hr LC50 of DDT speeded up learning of the conditioned response whereas a comparable concentration of methoxychlor had no affect. Since concentrations actually present in our tanks may have been much less than this, it is possible that field application of these insecticides may produce changes in learning capabilities of wild fish. However, the duration of field application is rather short, although the consumption by fish of dead and dying insects could raise the effective dose considerably. The importance of any such changes in learning ability upon the survival of wild fish remains to be shown.

In conclusion, it is apparent that insecticides can alter the learning capabilities of Atlantic salmon parr if the dose is sufficient, but alterations induced are apparently not permanent. More studies in this general area of behaviour using very low concentrations of insecticide are warranted since, though learning speed may not be affected, the larger number of "miss" responses induced by our low concentrations indicate that the learning behaviour of the fish is being affected in some as yet unknown manner.

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NOTES

Use of Continuous Recording Salinity–Temperature–Pressure Instrumentation at Ocean Station P (50N, 145W)

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COLLINS, C. A., AND D. A. HEALEY. 1972. Use of continuous recording salinity–temperature–pressure instrumentation at Ocean Station P (50N, 145W). J. Fish. Res. Bd. Canada 29: 323–327.

The operational precision of STP instruments for salinity and temperature was estimated as 0.07 ppt and 0.07 C, respectively. Correction of electronically digitized data for instrument response constants failed to improve the quality of the data. However, a response constant of 1 sec would remove the salinity inversions associated with large temperature gradients. Smoothing of STP data with a numerical taper about 2-db wide and decimation to 2-db intervals seemed appropriate for 0.2 sec sampling rates.

COLLINS, C. A., AND D. A. HEALEY. 1972. Use of continuous recording salinity–temperature–pressure instrumentation at Ocean Station P (50N, 145W). J. Fish. Res. Bd. Canada 29: 323–327.

Les auteurs ont estimé à 0.07 ppt et 0.07 C respectivement, la précision opérationelle des appareils STP pour les mesures de salinité et de température. La correction des données chiffrées électroniquement en vue d'établir des constantes de réponse des appareils n'a pas réussi à améliorer la qualité des données. Cependant, une constante de réponse d'une seconde éliminerait les inversions de salinité associées aux gradients élevés de température. La rectification des données STP à l'aide d'un effilement numérique d'une largeur d'environ deux db et une décimation de deux intervalles db semblent appropriées pour des taux d'échantillonnage de 0.2 secondes.

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FROM 1968 to 1970, continuous recording salinity–temperature–pressure (STP) instruments (Bissett-Berman Model 9006 and 9040 STDs) were introduced at Ocean Station P (50N, 145W). The method in which these instruments are used depends not only on their characteristics (accuracy, precision, and time response) but also on the nature of the scientific program. The program at Station P is a climatological one so that precision is important. STP data must also be compatible with the historical (Nansen bottle) data from Station P. These requirements suggest the following criterian for STP data: profiles should be equivalent to profiles obtained with Nansen bottles separated about two meters vertically. This note summarizes our efforts to (i) estimate the operational precision of the STP, and (ii) process STP data into a format compatible with Nansen bottle data.

The advantages and disadvantages of present STP instruments seem to be well known. The calibration must be checked continuously and large salinity errors occur when temperature changes rapidly. However, continuous vertical profiles are obtained and since wire angles are not important, sampling can be done in bad weather (on the weatherships, we have obtained STP profiles in winds up to 30 knots vs 20 knots for Nansen bottles). This capability is necessary in winter months. Furthermore, STP profiles can be completed in less time than Nansen bottle profiles.

Operational precision of STP results — An operational precision for our historical Nansen bottle data is estimated as two standard deviations (2σ) of 4000 m results (Robertson and Glennie 1968).

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This was 0.020 ppt and 0.028 C for salinity and temperature, respectively.

To estimate the precision of our STP instruments, we made many comparisons between Nansen bottle and STP profiles. The data in Fig. 1 were representative of our efforts, e.g., profiles were incorporated from various cruises and at different lengths of time from factory recalibration. Results are given for each of three STP instruments. The differences were grouped at standard bottle depths, although they were calculated at the accepted Nansen bottle depths. Also, since both types of profile were obtained sequentially, only some surface and deeper values were compared. Values for the standard deviation of temperature difference fluctuated widely above 300 m due to large horizontal and vertical temperature gradients. Below 250 m, there was less fluctuation; the maximum value was 0.068 C and differences between results for the three STP instruments were not significant. A pooled standard deviation for temperature differences below 250 m was 0.035 C. Assuming no errors in depth (pressure) measurement, the precision of the STP results can be estimated by

$$\sigma^2_{STP} = \sigma^2_{STP-Nansen} - \sigma^2_{Nansen};$$

and this means that the precision of the STP temperature measurements was 0.067 C, 240% greater than that for Nansen bottles.

Profiles of the standard deviation of the salinity difference between Nansen bottle and STP instruments did not fluctuate as much as those for temperature. The maximum standard deviation was 0.055 ppt and the minimum 0.010 ppt. The pooled standard deviation for all salinity data in Figure 1 was 0.035 ppt. This means that the precision of the STP salinity was 0.069 ppt; this was 340% greater than that for Nansen bottle data.

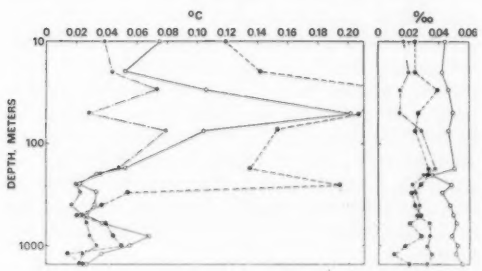

FIG. 1. Profiles of standard deviation of difference between Nansen bottle and STP results for three instruments, 9006–1 (●), 9006–2 (○), and 9040 (*). Each profiles was the result of about 12 sequential Nansen bottle and STP casts at Station P.

At depth we found it difficult to check the calibration of the pressure sensor with unprotected thermometers. During a 6-week period in May and June, 1969, the results of 32 comparisons at depth gave a mean difference of 5 db (STP greater than thermometric pressure) and a standard deviation of 25 db.

Processing electronically digitized STP data — The STP data are usually recorded with a strip chart recorder. We manually digitize these records by reading values of salinity and temperature at sufficient depth intervals and to the nearest 0.01 C, 0.01 ppt, and 1 m[1] to characterize the trace, the digitization continuing until computer plotted and analog traces are coincident. At Station P and for a 300 m cast, we have found between 20 and 70 depths sufficient.

The signals which drive the analog strip chart recorder can be electronically digitized and recorded on magnetic tape or punched paper tape. One such unit, the digital data logger (DDL) (Bissett-Berman Model 8114) can be purchased from the manufacturer of the STP. We have also digitized STP output using a small computer and an electronic counter (Huyer and Collins 1969). Table 1 compares the resolution and cycle time for the two digitizers. Although the DDL had greater resolution and was faster, it was less flexible and not as reliable as the small computer.

Jones' (1969) method of processing DDL tapes was found suitable for use with data from the Eastern Tropical Pacific. Jones' scheme is outlined as follows: (i) translate the data, accepting only data within realistic bounds; (ii) delete all records for which depth does not increase; (iii) tapering, consisting of a running mean of five values (since usually five values per meter) followed by a running mean of

TABLE 1. Comparison between characteristics of digitizing methods for STP data.

	Analog Trace	DDL	Small Computer
Resolution of			
Temp C	0.01	0.009	0.02
Salinity ppt	0.01	0.00067	0.003
Pressure db	1/5/10[a]	0.03	1
Total time to obtain finished product, (man-hours)	3–4	1	1

[a]On 300, 750, 1500 db scales, respectively.

[1]The analog trace scales pressure to depth by dividing the former by 1.0048 db/m.

three values; (iv) decimate, accepting only every third value; (v) interpolate or average to obtain only one observation per meter and at least one observation per meter; (vi) use your own judgement to make the shape of the salinity profile acceptable; (vii) correct salinity values for temperature gradients; (viii) correct salinity values to agree with other data. Figure 2 illustrates the effect of items (iii) and (iv) on DDL data. The profiles become less noisy on the application of each step. However, the salinity inversions (not real) associated with strong temperature gradients remain.

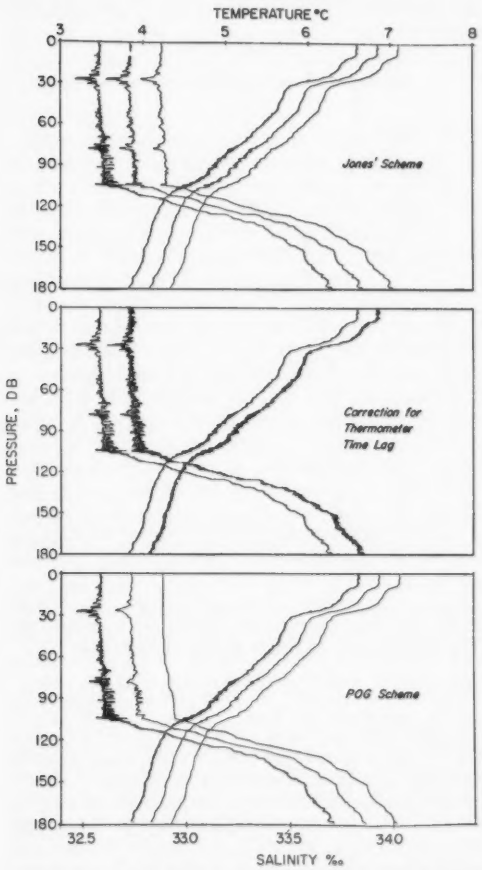

FIG. 2. Digital data logger (DDL) processing schemes. In each panel temperature profiles are to the right and salinity profiles are to the left at the surface. Within each group of temperature and salinity profiles, the profile farthest to the left was obtained directly from DDL output. Successive temperature and salinity profiles were obtained numerically from the DDL output using methods explained in the text and are displaced 0.25 C and 0.15 ppt, respectively, to the right. The DDL sampled every 0.2 sec.

Graefe (1968) outlined another method of processing DDL data. Graefe, using all acceptable data, corrects for thermometer lag coefficients, orders temperature and salinity according to increasing depth, averages to 2-m intervals, and finally smooths temperature and salinity in the depth domain and depth in the time domain. Output is in a bathythermograph format at 2-m intervals. Advantages of Graefe's scheme vs Jones' is that all data are used and a correction for the rate of change of temperature with time is made when this information is still available. Unfortunately, both methods require medium-sized computers.

We have examined these and alternative DDL processing schemes. Since the DDL records data as a function of time, correction for thermometer lag coefficients should be possible. The true temperature, θ, is given by:

$$\theta = T + \tau \dot{T}; \tag{1}$$

where T is measured temperature and τ an instrumental response constant equal to 0.35 sec. The true salinity, S, is obtained from a formula derived by Gaul (1968),

$$S = S^* [1 - \tau K_r K_g \dot{T}]; \tag{2}$$

where S^* is measured salinity and K_g and K_r are, respectively, a conductivity coefficient and conductivity ratio coefficient. Figure 2 illustrates DDL output which has been corrected using (1) and (2). Corrected profiles (right) are noisier than uncorrected profiles and the salinity inversion at the top of the thermocline persists. For these reasons, as well as the fact that corrections to salinity and temperature are usually quite small, we make no attempt to correct DDL data for the effect of the thermometer lag coefficient.

Figure 2 illustrates the effects of a scheme for numerical processing of DDL records which we found suitable for use with a small computer. After removing unrealistic parameter values, all records are smoothed in the time domain using a numerical taper of about four seconds width. Data are then interpolated or averaged to 2 db intervals and salinity is required to be a monotonic increasing function of pressure in the upper 100 m. Finally (not shown in Figure 2), salinity values are corrected to agree with Nansen bottle results.

Using the small computer and electronic counter rather than the DDL, the STP is sampled and processed "on-line." Ideally, this means that sensor

errors can be applied to the data as it is gathered. However, in practice, we found it feasible only to correct the pressure sensor for a constant error. We also programmed the computer so that data are collected only when pressure increases.

The counter averages the signal (pressure, temperature, or salinity) for 1 sec which eliminates further numerical smoothing of the data. Because the signals are sampled sequentially, vertical profiles and temperature–salinity pairs may be distorted when gradients are large; in practice we have not noticed this. Salinity inversions at the top of the thermocline do persist in the computer output and these require editing; this may include correction for salinity errors and decimation or interpolation of data to 2-db intervals.

Comparison of processed STP data — On a single 750-db cast on June 1, 1969, the signals from the STP unit were recorded with a strip chart recorder, a digital data logger (DDL), and a small computer. Data were processed as described above. However, the 73 points taken from the strip chart were interpolated to 2-db intervals so that the data would be compatible with those from the DDL and the small computer. Figure 3 and Table 2 compare the results.

In general, agreement was good. It was possible to distinguish between the salinity and temperature profiles only below 150 db (Fig. 3). Here, profiles from the strip chart recorder were consistently 0.01 ppt lower and 0.02 C higher for salinity and temperature, respectively.

Agreement was best between small computer and DDL results and worst between small computer and strip chart results (Table 2). DDL salinities and temperatures were, respectively, 0.005 ppt and 0.007 C lower than small computer results. These differences between DDL and small computer can be in part attributed to: (i) the small computer takes 3 sec to sequentially sample pressure, temperature, and salinity vs 0.2 sec for the DDL; (ii) a bias in the frequency standard of one of the digitizers. The combination of (i) and (ii) with a one-half Hertz error (DDL less than small computer) yield a difference of –0.004 ppt and –0.009 C, DDL minus small computer, in good agreement with the values in Table 2. The differences between strip chart and DDL data, –0.009 ppt and 0.02 C for salinity and temperature, respectively, could be attributed to an offset in the alignment of the strip chart recorder.

Differences in geopotential anomaly between data sets are easier to interpret as the distance required between stations for a velocity of 1 cm/sec; for geopotential anomalies of 0.09 and 0.06 J/kg a separation of 81 and 54 km, respectively, would result in a geostrophic current of 1 cm/sec (at the surface with respect to 750 db). The potential energy anomaly, 0.41×10^8 ergs/cm^2 indicates a transport of 0.4 Sverdrups above 750 db between stations (Table 2).

The standard deviation between the data sets (Table 2) can be considered as a sum of quantization errors and other errors. Quantization errors accounted for 50% of the standard deviation of temperature differences and 30% of the standard

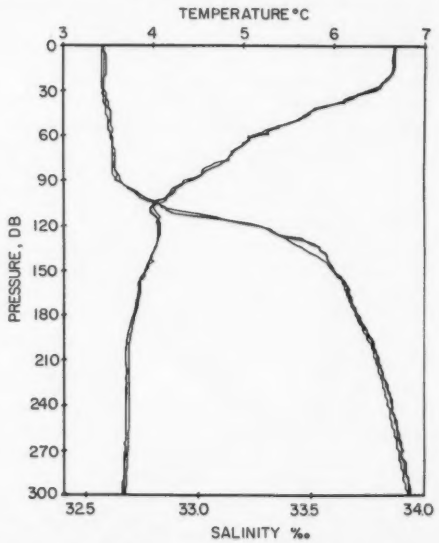

FIG. 3. Comparison of processed DDL, small computer and strip chart recorder data for a single cast. The temperature profile is to the right at 0db.

TABLE 2. Comparison of processed STP data for a 750-db cast made on June 1, 1969, at 50 N 145 W. Analog signals were recorded with a strip chart recorder (SC), a digital data logger (DDL), and a small computer (HP) and processed as described in the text.

		SC-DDL	SC-HP	DDL-HP
Temp	mean	2.0	1.3	–0.7
10^{-2} C	SD	1.9	2.6	1.5
Salinity	mean	–0.9	–1.4	–0.5
10^{-2} ppt	SD	1.2	1.2	0.7
Geopotential anomaly at 750 db, 10^{-2} J/kg		6	9	3
Potential energy anomaly at 750 db, 10^6 ergs/cm^2		31	41	10

deviation of salinity differences. Note that the standard deviation of the difference of the electronic digitizers was less than that involving the human-digitized strip chart. This is to be expected as not only were quantization errors larger for strip chart results, but human errors (including the tendency of the eye to smooth) should be greater than electronic errors. Indeed, salinity results indicated that (nonquantization) errors associated with the analog trace, 0.01 ppt, were twice those obtained with the electronic digitizers, 0.005 ppt. On the other hand, strip chart errors were equivalent to those obtained from the small computer for temperature results, 0.015 C, vs about 0.005 C for the DDL.

Discussion — From the results in the first section, we conclude that the operational precision of the STP was not acceptable. This confirms the experience of others (Morrison MS 1971). To reduce the precision of the STP results to an acceptable level, we found it necessary to continuously check the calibration of the STP during field use.

At sea, we calibrate the STP by placing a Nansen bottle immediately above the STP and tripping it when the STP is at its maximum depth. In addition, a surface Nansen bottle sample is obtained while the STP is at the surface, so that two values of temperature and salinity can be compared for each cast. At Station P, the usually homogeneous surface layer and small vertical gradients of temperature and salinity below 250 db facilitate such a comparison. Also, during each survey, a number of hydrographic casts are made immediately before or after the STP casts resulting in vertical profiles of temperature and salinity for field calibration of the STP. These profiles also check the linearity of the salinity and temperature difference with pressure which is implicit in the two-point method. STP values can then be corrected to make the two data sets agree more closely.

It would seem that electronic digitization and recording of STP data would allow compensation for instrumental response constants. But our attempts to do this were unsuccessful. A reason for this might be the different response constants for the two thermometers used to compensate conductivity; 0.35 and 1.0 sec (Morrison MS 1971). Pingree (1971) has also indicated that the system response time probably lies between 1–2 sec. To remove the salinity inversions illustrated in Fig. 3 using equation (2), a response constant of 1 sec was required. But even with this response constant, compensated results were noisier than the raw data.

Since correction for response constants is not possible, the numerical scheme for processing digitized STP data consists largely of the selection of an appropriate numerical taper. Roden (1968) suggested a binomial taper, Jones (1969a) utilized a series of equally weighted averages, and Graefe (1968) and ourselves used a Lanczos-squared taper. Any such taper is appropriate. For the width of the taper, we chose 4 sec as this corresponds to about 2 db at a lowering rate of 30 m/sec and hence meets the criterion stated in the introduction. (Note, too, that this is consistent with the mixing length of the Nansen bottle, 2.8 m, Weiss 1971). Jones' taper was almost as large as ours while Graefe and Roden proposed tapers of about 14 db and 130 db, respectively. At Station P, such wide tapers might be suitable below 300 db. However, above 300 db, the 2-db wide taper is better to use, especially when archiving and reporting data.

Of continuing concern are the subjective steps in processing STP data. We include in this category our requirement that salinity be a monotonic, increasing function of pressure. We apply this requirement routinely only to Station P data, and at other stations only to salinity inversions associated with thermoclines. We attempt to confirm other salinity inversions by obtaining "up" traces and using Nansen bottles. Nevertheless, some uncertainty remains, e.g., STPing with present instruments remains somewhat of an art.

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Pathological Effects in Formalin-Treated Rainbow Trout (*Salmo gairdneri*)

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SMITH, C. E., AND R. G. PIPER. 1972. Pathological effects in formalin-treated rainbow trout (*Salmo gairdneri*). J. Fish. Res. Bd. Canada 29: 328–329.

When rainbow trout (*Salmo gairdneri*) were exposed to 167 and 250 ppm formalin for 1 hr, moribund fish showed severe histopathological changes in gill epithelium. Hematocrit values and numbers of immature red blood cells were increased, suggesting a physiological response to hypoxia. The results are discussed in relation to the probable cause of death.

SMITH, C. E., AND R. G. PIPER. 1972. Pathological effects in formalin-treated rainbow trout (*Salmo gairdneri*). J. Fish. Res. Bd. Canada 29: 328–329.

Après exposition pendant une heure à des concentrations de 167 et 250 ppm de formaline, les truites arc-en-ciel (*Salmo gairdneri*) moribondes exhibent des lésions histopathologiques de l'épithélium branchial. Les valeurs de l'hématocrite et le nombre d'érythrocytes augmentent, signe d'une réponse physiologique à l'hypoxie. La cause probable de la mort est analysée à la lumière de ces résultats.

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RAINBOW trout are reported to be sensitive to formalin, which is used in the treatment of protozoan and other external parasites of hatchery-reared fish (Fish 1947; Rucker et al. 1963; Wood 1968). Formalin concentrations of 167–250 ppm administered over a 1-hr period sometimes result in mortality (Wedemeyer, 1971; R. G. Piper and C. E. Smith unpublished data). Rucker (1962), in a progress report, briefly described histopathological changes in the gills of rainbow trout exposed to 250 ppm formalin for 2 and 3 hr, and to 2000 ppm for 1 hr.

To our knowledge, no previously published report has described and illustrated changes in various fish tissues as a result of formalin treatment. Because of this, the present experiment was designed to determine hematological and histological changes in rainbow trout associated with formalin treatment.

Methods — Two groups of 100 rainbow trout (Ennis, Montana, strain), averaging 6.7 inches in length, were exposed to 167 ppm formalin for 1 hr in concrete troughs containing 760 gal of water. Water temperature was 12.8 C. Another group of 100 fish served as controls. In another experiment, two groups of 100 fish were exposed to 250 ppm for 1 hr.

After the exposures, the troughs were immediately drained and refilled with fresh water. Dissolved oxygen content of the water was monitored over the 1-hr period with a YSI oxygen meter, and remained relatively constant at 7–8 ppm.

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Within 3 hr of exposure, five moribund fish were taken from each group for histological examination. Five control fish were killed. Gill, kidney, liver, spleen, brain, pseudobranch, intestine, pyloric caeca, and stomach tissue were sectioned and stained with hematoxylin and eosin, using standard histological techniques.

Hematocrits were determined on five moribund fish from each treatment, and on five controls (Hesser 1960). Blood smears were prepared and stained by the Leishman–Giemsa method (Smith 1968). The average mortality for fish subjected to 167 and 250 ppm formalin was 4.0 and 6.0% respectively. Death usually occurred 2–4 hr after exposure.

Results — Severe pathological changes were observed in the gills of treated fish. Gill epithelium was often severely swollen, and in some instances, had completely desquamated from the lamellae, leaving only the blood capillary and supportive pillar cells (Fig. 1–3). Leucocytic infiltration was occasionally noted. Some epithelial cells showed cloudy swelling, and others had pyknotic and fragmented nuclei. Blood plasma sometimes accumulated between gill epithelium and blood capillaries (Fig. 3), and in certain areas hemorrhage was evident. Histologically, there was no difference between the gills of fish treated with 167 ppm formalin and the gills of those treated with 250 ppm.

Other histological changes noted in both groups of treated fish were: nuclear swelling and hypertrophy of pseudobranch epithelium (Fig. 4, 5); hyperplasia and hypertrophy of adrenal cortical

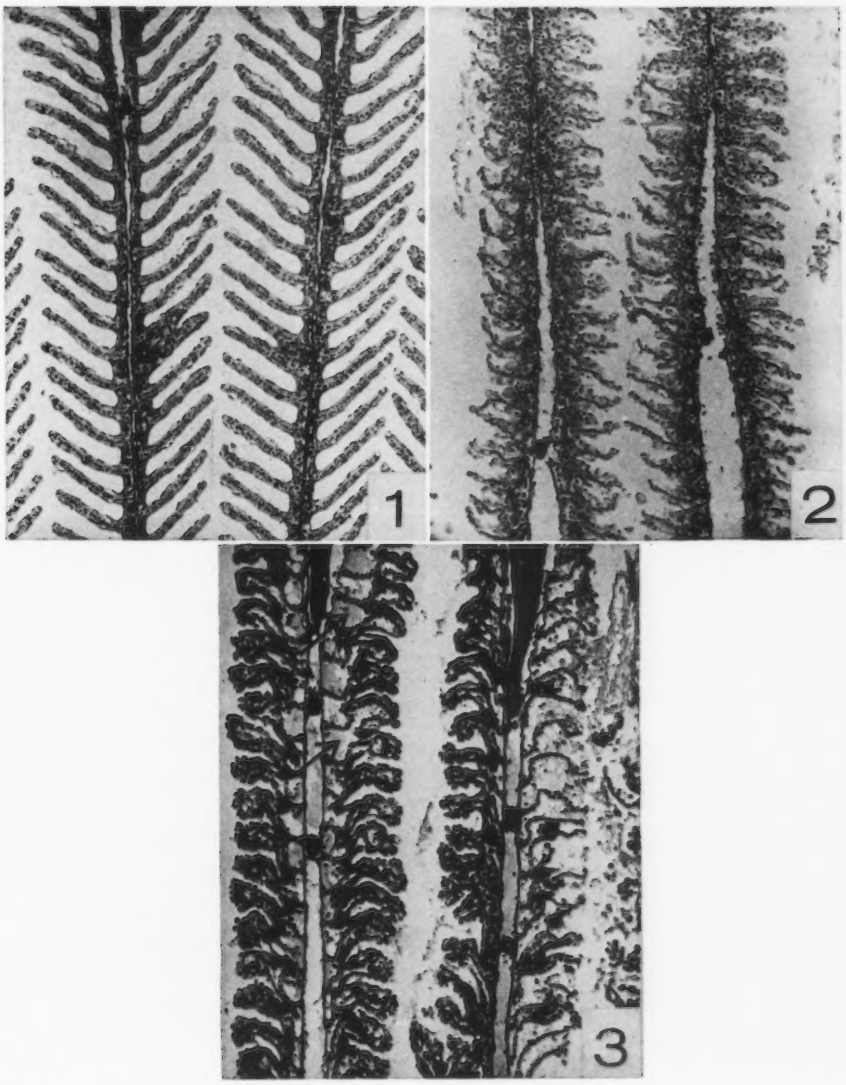

FIG. 1–3. Gill lamellae. 1, from untreated trout. 2, 3, extensive swelling and desquamation of epithelium from treated trout, and, 3 only, accumulations of plasma at bases of several lamellae. (note arrows) × 140.

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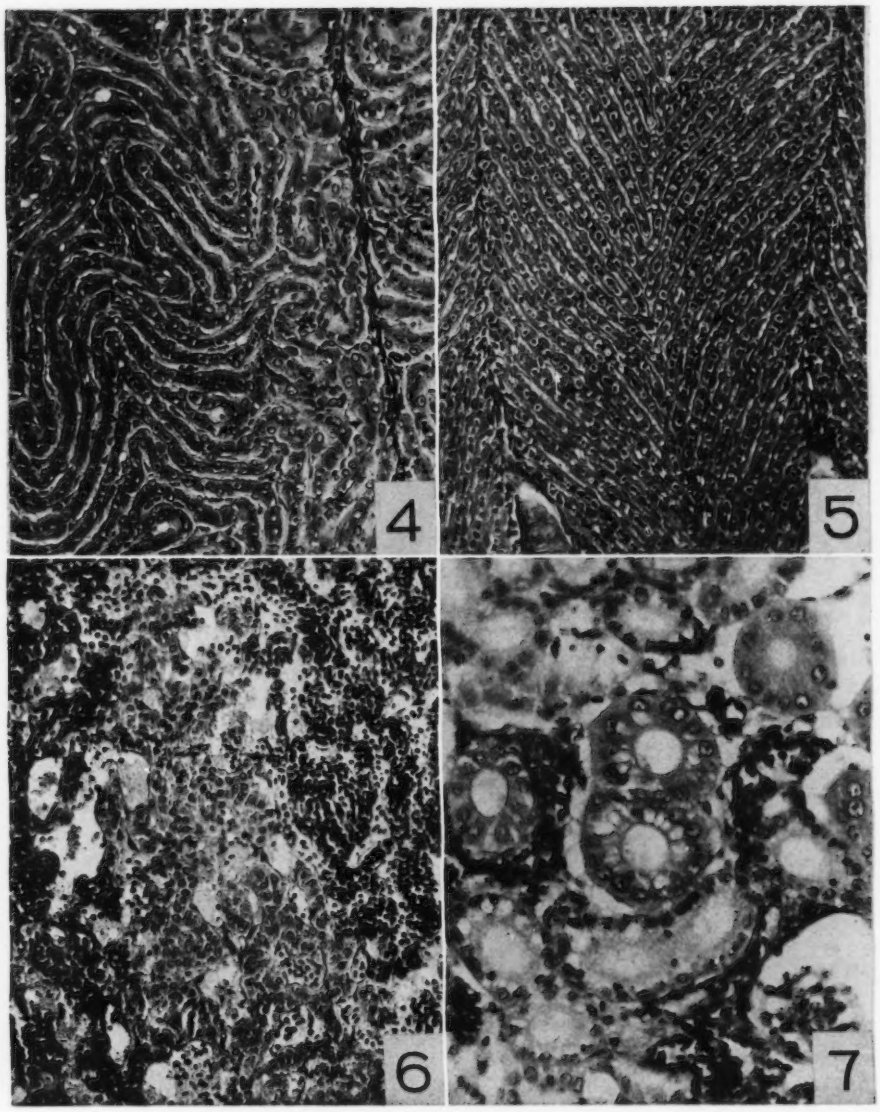

FIG. 4. Hypertrophy and nuclear swelling of pseudobranch epithelial cells. × 140.
FIG. 5. Normal pseudobranch. × 140.
FIG. 6. Hyperplasia of adrenal cortical tissue. Note hypertrophied cells with prominent nucleoli. × 140.
FIG. 7. Hydropic degeneration and nuclear swelling of renal tubule epithelium. × 315.

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cells (Fig. 6); reduction of lymphoid tissue in spleen, and congestion of blood sinusoids in kidney tissue. Nuclear swelling and hydropic degeneration of renal tubule epithelium occurred in fish exposed to 250 ppm (Fig. 7).

Hematocrit values of both groups of treated fish were significantly elevated ($P < .05$). Fish subjected to 167 ppm formalin had an average hematocrit value of 49.2%, compared with 41.4% for the controls; those treated with 250 ppm, 46.0% vs. 36.0%. Examination of blood smears revealed an increase in the number of immature red blood cells in treated fish (16.4% vs. 10.7% for controls). Formalin treatment also resulted in destruction of some erythrocytes, as evidenced by hemolysis in hematocrit tubes.

Discussion — The severe pathological changes we observed in the gills of formalin-treated trout were of sufficient magnitude to result in dysfunction of gill epithelium, rendering the fish unable to osmoregulate. Such changes would account for the impairment of oxygen–carbon dioxide exchange, and for the hypoxia reported by Wedemeyer (1971) in two species of salmonids.

Since red blood cell counts and hematocrits increase in fish in response to low oxygen environments (Hall et al. 1926; Prosser et al. 1957; C. E. Smith unpublished data), the increased hematocrit and number of red blood cells observed in formalin-treated trout suggest a response to hypoxia resulting from severe damage to gill respiratory epithelium. The fact that plasma protein levels are not reduced during formalin stress indicates that these changes are not due to hemoconcentration.

Wedemeyer (1970) outlined physiological and biochemical changes that occur in animals following stressful environmental changes. He also cited evidence showing that the response of lower animals to stress is similar in many ways to that of higher animals; namely, endocrine imbalance, acute stimulation of adreno-cortical function, and lymphoid involution.

The adrenal cortical hyperplasia and reduction in splenic lymphoid tissues we observed were probably responses to physiological changes due to stress induced by formalin treatment.

The degree of formalin toxicity in trout has been thought to be associated with hardness and buffering capacity of the water in which fish are treated. However, data we have accumulated from state and federal hatcheries throughout the United States suggest that toxicity depends more on species, and even strains of trout, than on water chemistry (R. G. Piper and C. E. Smith unpublished data).

It seems apparent that death of formalin-treated trout is due to severe gill pathology, resulting in their inability to maintain osmotic and acid-base balance. This is further complicated by hypoxia and the inability of the fish to maintain normal metabolism.

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Ecological Notes on a Lake-Dwelling Population of Longnose Dace (*Rhinichthys cataractae*)

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GEE, J. H., AND K. MACHNIAK. 1972. Ecological notes on a lake-dwelling population of longnose dace (*Rhinichthys cataractae*). J. Fish. Res. Bd. Canada 29: 330–332.

Longnose dace were found from early July to September in onshore waters on the east side of Hecla island in the southern basin of Lake Winnipeg. They were most abundant on rocky substrates, where they spawned in early July. It is suggested that at other times of the year these fish occupy deep channels between islands where current is present. While in onshore waters fish less than 5 g adjusted their buoyancy by altering swimbladder volume in response to presence or absence of wave action. Swimbladder volume was similar to that of river-dwelling populations of this species.

GEE, J. H., AND K. MACHNIAK. 1972. Ecological notes on a lake-dwelling population of longnose dace (*Rhinichthys cataractae*). J. Fish. Res. Bd. Canada 29: 330–332.

On trouve des goujons à long nez à partir du début de juillet jusqu'en septembre près de la côte orientale de l'île Hecla, dans le bassin méridional du lac Winnipeg. Ils se rassemblent sur les fonds rocheux, où ils frayent au début de juillet. Ils passent le reste de l'année, semble-t-il, dans les chenaux profonds, entre les îles, où il y a du courant. Durant leur séjour près de la côte, les goujons pesant moins de 5 g ajustent leur flottabilité suivant l'action plus ou moins forte des vagues, en changeant le volume de leur vessie gazeuse. Le volume de la vessie gazeuse est le même que celui des populations fluviatiles de l'espèce.

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ALTHOUGH much is known about stream-dwelling populations of longnose dace (*Rhinichthys cataractae*), little is known about lake-dwelling populations. This report provides information on the distribution and abundance in relation to substrate of a population of dace in onshore waters of Lake Winnipeg and on time of spawning, food consumed, and effect of wave action on buoyancy.

In streams in southern Manitoba reproduction occurs in the last half of May in water velocities exceeding 45 cm/sec with a substrate of large stones (Bartnik 1970). Fry emerge in June, occupy still waters until they are 25–30 mm long, and then move into riffles exceeding 45 cm/sec. Diet is mostly aquatic insect larvae and nymphs (Gibbons MS 1971). While in still water fry are neutrally buoyant but buoyancy decreases with increasing size (Gee 1968; Gee and Northcote 1963). The fish can adjust their buoyancy by altering the volume of the swimbladder in response to a change in water velocity.

Materials and methods — Information was collected on dace captured along the east shore of Hecla Island in the southern basin of Lake Winnipeg (Fig. 1). The positions of Hecla and Black islands result in three constricted channels, those between Hecla and Black islands and between Black Island and the east shore of the lake being deeply scoured to depths of 22 and 37 m, respectively. The third channel is shallow (1–2 m). Current in the deep channels, caused to some extent

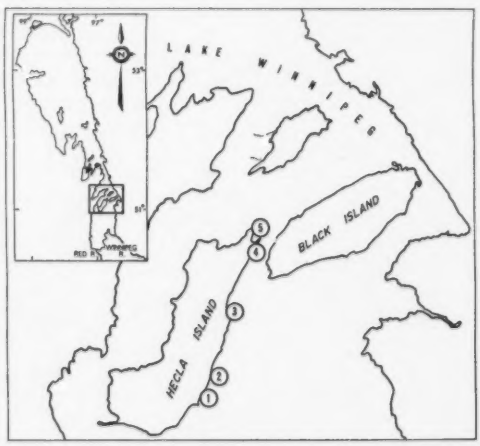

FIG. 1. Lake Winnipeg, Manitoba (inset) and positions of Hecla and Black Islands with locations of sites 1–5.

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by drainage of waters northward from the Red and Winnipeg rivers and by wind-generated seiches, can be considerable.

Collections for dace, using a beach seine (5 meshes/cm), were made at 5-week intervals or less from August to October 1968 and from May to July 1969 to provide information on distribution and abundance in onshore waters. Only waters 1 m or less in depth and no further than 10 m from shore were sampled. Normally an area to be sampled was seined only once. But on one occasion, to assess the efficiency of seining, a barrier net (5 meshes/cm) was used to enclose an area which was then seined repeatedly until no further fishes were captured. A comparison of catches from the two methods revealed at least half of the dace present were captured with only one seine haul. Seining was carried out at five sites (Fig. 1), each with one of the three following types of substrate: (a) > 80% sand or fine gravel (< 2 cm diameter, sites 1, 2, 5), (b) >80% gravel or small stones embedded in sand (3–12 cm diameter, site 3), and (c) 100% large rocks (8–30 cm diameter, site 4).

Captured dace were preserved in 10% formalin and later transferred to 40% isopropyl alcohol for examination of stomach contents, sexual maturity, and swimbladder volume. Contents of the anterior portion of the alimentary canal were identified to order and their dry weight (± .001 g) was determined. Time of spawning was determined on the basis of weight of gonads (± .001 g, females only) expressed as a percentage of body weight. Variation in swimbladder volume (± .001 ml, Gee 1968) relative to body weight was recorded for some fish to determine if changes in buoyancy occurred between those captured on calm and windy days (waves present). Length frequencies were used to age fish into years 0, 1, 2, and 3+.

Results and discussion — Dace were abundant in July and early August on the rocky substrate at site 4 and were either rare or absent on the remaining substrates (Table 1). Density of dace was lower in September and none were collected at any of the sites in October or May. During July and early August, the density of dace at site 4 varied between 2.3 and 2.8/10m², except that on August 1 density was 9.6/10 m². This was the only day that collections were made when large waves were breaking on shore. Here the density of dace approached that found in rapids of streams (Bartnik 1970). This higher density did not appear to be the result of increased vulnerability to seining and could represent a movement of dace from waters just offshore to areas of turbulence near shore.

There are several indications that dace spawn near shore at site 4: (a) the substrate is similar to that on which stream-dwelling populations spawn, (b) most of the dace captured were adults (age 2 years and older, Table 1), (c) gravid females and ripe males in spawning colour were present in July, and (d) newly emerged fry were captured in abundance by dipnet close to shore under cover of overhanging vegetation on August 1. As newly emerged fry must come to the surface and gulp air to fill their swimbladders (Gee 1968), spawning in shallow onshore waters may be necessary for fry to be able to move up to the surface prior to filling their swimbladders.

Weights of gonads of females, expressed as percentages of body weight, suggested a spawning period from late June to mid-July. On July 2 eight fish were examined (mean 10.5 ± 3.23[1]); on July 15 five (mean 11.0 ± 4.84); and on July 23 five (mean 6.5 ± 1.84). The development of gonads on July 2 and 15 is similar to that found by Bartnik (1970) for spawning dace in Mink River (Manitoba). The finding of newly emerged fry on August 1 confirms this time of spawning as dace hatch, leave the substrate, and fill their swimbladders within 16 days (Gee 1968). Thus, this population spawns 5–7 weeks later than those in streams. Water temperature undoubtedly plays an important role as

[1]One standard deviation of mean

TABLE 1. Densities of dace (excluding fry) on different substrates on the east shore of Hecla Island.

	Sand and fine gravel (sites 1, 2, 5)			Gravel and small stones (site 3)			Large rocks (site 4)		
	Area seined (m^2)	no./10 m²	% adults	Area seined (m^2)	no./10 m²	% adults	Area seined (m^2)	no./10 m²	% adults
July 2	107	0		90	.6	20	252	2.8	90
15	121	.2	100	81	.3	100	75	2.5	79
23							108	2.7	97
Aug. 1	59	0					81	9.6	100
7	153	.1	100	56	.2	0	100	2.3	100
Sept. 9	203	0		32	.6	100	27	.7	100

spawning in streams occurs when daily maximum temperatures exceed 15 C (Bartnik 1970). At site 4, the following mid-day surface temperatures (degrees C) were recorded: May 21, 5, July 2, 15.5, July 15, 19.5, July 23, 20.

The sex ratio of adult dace did not change during or after spawning but amongst age II fish, males predominated (ratio 47:77) while most of the older fish were females (ratio 73:22), a finding similar to that of Reed (1959).

Diet of dace was similar throughout July and August, and from 36 dace examined the percentage contributions of the following groups to the total weight of food eaten were: Diptera larvae, 52; Trichoptera larvae, 26; algae, diatoms, sand, 7; unidentified, 15.

Buoyancy decreased with increasing size of fish (Fig. 2). Those captured on calm days were, on the average, twice as buoyant as those captured on August 1, a windy day, except that there was no difference in the largest group. In the laboratory Gee (unpublished data) has found that individuals from this population made significant adjustments of buoyancy in response to a change in water velocity but that such adjustment was dependent on size. Fish exceeding 4 g were unable to adjust buoyancy significantly.

Swimbladder volume of fish less than 1.5 g varied between .003 and .028 ml, a range similar to that found in populations in the Fraser River (British Columbia), Moose Lake, Roseau and Rat rivers (Manitoba). But amongst heavier fish variation occurred between .004 and .048 ml, a range similar to that for the above river-dwelling populations but generally below that for fish from Moose Lake, which varied from .030 to .290 ml (Gee 1968). The smaller swimbladder volume of Lake Winnipeg dace than for those from Moose Lake suggests that when not in onshore waters they occupy areas of current offshore from site 4 between Hecla and Black islands. There is a marked preference for current in this species (Gee and Northcote 1963) and the initial selection of such an environment by fry could occur within the first 6 weeks of life as in streams (Gibbons MS 1971).

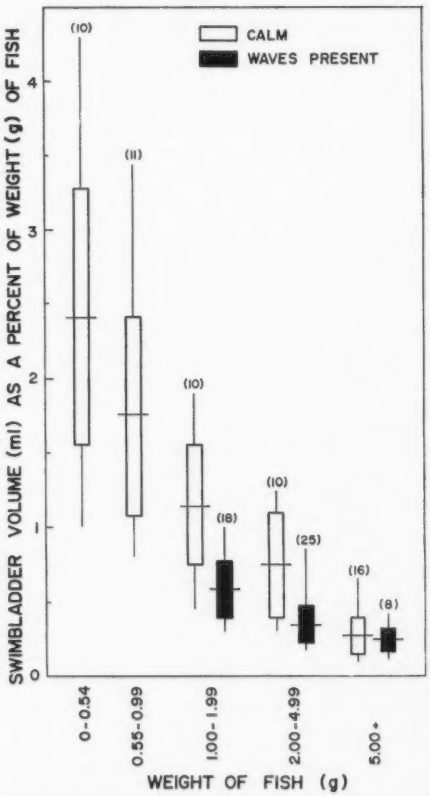

FIG. 2. Buoyancies of some dace captured on rough and calm days. Each horizontal line represents the mean, bars are one standard deviation above and below the mean, and vertical lines indicate the range. Numerals in parentheses are numbers of fish examined.

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Aerobic Microflora of the Bluefish (*Pomatomus saltatrix*) Intestine[1,2]

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NEWMAN, J. T., JR., B. J. COSENZA, AND J. D. BUCK. 1972. Aerobic microflora of the bluefish (*Pomatomus saltatrix*) intestine. J. Fish. Res. Bd. Canada 29: 333–336.

From 65 bluefish caught in Long Island Sound, 433 isolates of bacteria from the intestinal contents were assigned to various groups, the most abundant being *Vibrio*, *Pseudomonas*, Enterobacteriaceae, and *Achromobacter*. Unidentified fermenters, yeasts, and strains of *Flavobacterium*, *Micrococcus*, and *Bacillus* were found also. In each group, two or three biotypes predominated. Flagellar arrangements and biochemical characteristics are presented for the major groups of Gram-negative bacteria isolated. The majority of cultures required sea water for growth, and grew preferentially at 20 C. Relationships between these data and studies of the intestinal microflora of other marine fish are discussed. Generic and physiological similarities and differences as well as taxonomic difficulties encountered are considered.

NEWMAN, J. T., JR., B. J. COSENZA, AND J. D. BUCK. 1972. Aerobic microflora of the bluefish (*Pomatomus saltatrix*) intestine. J. Fish. Res. Bd. Canada 29: 333–336.

Nous avons identifié 433 isolats bactériens du contenu intestinal de 65 tassergals capturés dans le détroit de Long Island, la majorité appartenant aux groupes *Vibrio*, *Pseudomonas*, Enterobacteriaceae et *Achromobacter*. Nous avons de plus trouvé des ferments non identifiés, des levures et des souches de *Flavobacterium*, *Micrococcus* et *Bacillus*. Chaque groupe possède deux ou trois biotypes dominants. Nous décrivons la disposition des flagelles et les caractères biochimiques des principaux groupes de bactéries Gram-négatif. La plupart des cultures dépendent de l'eau de mer pour leur croissance, qui est optimale à 20 C. Nous comparons nos données avec les résultats de recherches effectuées sur la microflore intestinale d'autres espèces de poissons marins. Nous soulignons les points de ressemblance et de différence génériques et physiologiques, ainsi que les problèmes taxonomiques rencontrés.

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ALTHOUGH studies on the microflora of marine fish have been reported for over 60 years, the majority of these data concerned the exterior surfaces (slime, fillets) and were related to spoilage aspects. Few investigations have involved extensive studies of intestinal microbial populations, and none are available on the microflora of the bluefish, (*Pomatomus saltatrix*), a game fish and potential food source for man along the eastern coast of North America. Some of its migratory habits have been documented by Lund and Maltezos (1970). Bigelow and Schroeder (1953) described the bluefish as "the most ferocious and blood-thirsty fish in the sea, leaving in its wake a trail of dead and mangled mackerel, menhaden, herring, alewifes, and other species on which it preys." If microorganisms present in the gut are a function of the food ingested (Shewan 1961; Seki 1969), then the feeding habits of the bluefish may be significant in affecting the types present in the intestinal microflora. The present investigation was designed to provide information on the bacterial populations associated with bluefish intestine. These data will furnish a baseline for an indigenous species which may be of significance in future evaluations of disease or other abnormalities in natural or maricultured populations.

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Methods — A total of 65 fish were line-caught between August and November, 1963, in an area of Long Island Sound designated as The Race, approximately 8 km south of New London, Conn. between Fishers Island and Plum Island, New York. The intestines were removed within 2 hr, placed in sterile petri dishes, and packed in ice. Within an additional 24 hr, 5 cm of intestine containing digested food and small ingested fish were removed aseptically, and one loopful was streaked on a medium (CP) (Carlucci and Pramer 1957) containing 0.5% Gelysate (Baltimore Biological Laboratories), 0.01% yeast extract (Difco Laboratories), 0.001% $FePO_4$, and 1.5% agar in aged sea water. Plates were incubated aerobically at 20 C for 3–5 days. All colonies on each plate that exhibited cultural differences were inoculated into CP broth and restreaked on CP agar to ensure purity. Stock cultures were maintained on CP agar slants at 4 C.

Gram stains and general cell morphology served to identify the Gram-positive forms. All Gram-negative isolates were subjected to the taxonomic scheme of Shewan et al. (1960). Further differentiation included gelatin liquefaction and nitrate reduction using Nutrient Gelatin (Difco) containing 0.1% KNO_3, the production of H_2S and indole (SIM medium; Difco), and carbohydrate metabolism in MOF medium (Leifson 1963) with glucose. Fermentation of carbohydrates (cellobiose, lactose, galactose, maltose, mannitol, sucrose, and xylose) was determined using a modified sugar base medium of Leifson (1963), bromothymol blue (0.002%) being substituted for phenol red and agar being omitted. Antibiotic sensitivity was tested on CP agar employing discs containing 10 μg of oxytetracycline (Pfizer), 2.5 units of potassium penicillin G (Squibb), and the vibriostat 0/129 (Shewan et al. 1954). Discs of the latter were prepared by saturation in a 0.1% solution of 0/129 in acetone and drying at 37 C. Flagella stains (Leifson 1960) were made from 18–24-hr CP broth cultures. Catalase production was determined by adding one drop of 3% H_2O_2 to colonies which were oxidase negative.

All cultures were incubated in CP broth at 20 and 35 C, with turbidity recorded visually. Gross observations on the stenohaline nature of the isolates were made in CP broth prepared with sea water and distilled water.

Microorganisms found — From 626 colonies selected for study, representing all 65 fish, 433 out of 522 isolates were assigned as follows to various groups: *Vibrio*, 28.4%; *Pseudomonas*, 22.4%; Enterobacteriaceae, 21.4%; *Achromobacter*, 18.2%; unidentified fermenters, 3.0%; yeasts, 2.5%; *Flavobacterium*, 1.6%; *Micrococcus*, 1.4%; *Bacillus*, 0.9%. All yeasts except one were pink-pigmented, and presumed to be members of *Rhodotorula*. Many isolates could not be placed in a specific genus by the Shewan method, and were designated as enterobacteria or unidentified fermenters. Those classed as members of the family Enterobacteriaceae were distinguished by being oxidase negative, exhibiting polar flagellation, and producing acid from glucose. The oxidase test served as the basis for their classification as enteric types. A few polar-flagellated fermenters were insensitive to the vibriostatic agent 0/129, and considered separately as marine fermenters.

In each group, two or three microorganisms predominated (Table 1). Luminescent bacteria were found among the vibrios and the enterobacteria. They represented 2.3% of the 522 isolates examined. Three types were found within *Vibrio*, based on growth at 35 C, gelatinase activity, and nitrate reduction. Luminescent members of the Enterobacteriaceae were similar physiologically. None fitted the descriptions of Liston (1954) for flatfish isolates.

The pseudomonads were subdivided further into Shewan's Groups I–V. Based on MOF reactions, the following distributions were noted: Group I, 19.7% (19); Group II, 16.5% (16); Group III, 55.2% (53); Group IV, 8.3% (8).

In addition to the tests listed in Table 1, the four major groups of vibrios were subdivided by sugar reactions. All fermented mannitol, maltose, and galactose, while none fermented xylose. Two groups produced acid reactions from sucrose and lactose; three groups fermented cellobiose. These data indicate further subgroupings possible within the vibrios.

Approximately 60% of the fermentative *Achromobacter* isolated were found to be sensitive to penicillin. Thus, the larger percentage of these cultures were confirmed as *Achromobacter* by the penicillin sensitivity test. Those not inhibited were classed in this group because of other similarities. All nonfermentative *Achromobacter*, except one, were sensitive to penicillin.

Pseudomonas isolates which produced no change or an alkaline reaction in MOF medium were unaffected by penicillin. Three of the 21 oxidative strains of *Pseudomonas* were inhibited. Since these were polar-flagellated and oxidative in MOF, they could not be placed with the peritrichous *Achromobacter* or the bipolar-flagellated *Spirillum*, which produce no change in MOF medium. These three isolates sensitive to penicillin were grouped tentatively with *Pseudomonas*. The penicillin test was shown valid for the majority of bacteria for which it was appropriate.

The majority of vibrios exhibited polar monotrichous flagellation, although mixed flagellation was observed in more than one group and included multitrichous, subpolar monotrichous, and lateral monotrichous patterns. Pseudomonads and fermenters showed polar and lateral monotrichous flagellation. All bacteria placed in the Enterobacteriaceae possessed polar monotrichous flagella; this characteristic may be inconsistent with our taxonomic assignment.

TABLE 1. Morphological and physiological characteristics of isolates of the major groups of gram-negative bacteria found in the bluefish intestine.

	No. of isolates	Motility	Oxidase test	MOF (glucose)	Growth at 35 C	Gelatin hydrolysis	NO_3 reduction	H_2S production	Indole production	Catalase	Growth in distilled water medium
Achromobacter	6	−	+[a]	F[c]	−	−	+	−	−	+	−
	14	−	−[b]	F	−	−	+	−	−	+	−
	25	−	+	F	+	−	+	−	−	+	−
	4	−	−	Alk[d]	+	−	−	−	−	+	+
	9	−	+	O[e]	+	−	−	−	−	+	+
	4	−	+	O	+	−	+	−	−	+	+
	2	−	+	NC[f]	+	−	+	−	−	+	+
Enterobacteriaceae	3	+	−	F	+	+	+	−	+	+	−
	9	+	−	F	−	−	+	−	−	−	−
	57	+	−	F	−	−	+	−	−	+	−
	4	+	−	F	−	+	+	−	+	+	−
Fermenters	3	+	+	F	+	+	+	−	+	+	−
	8	+	+	F	−	+	+	−	+	+	−
Flavobacterium	2	−	−	O	+	−	−	−	−	+	+
	2	−	+	Alk	−	+	−	−	−	+	−
	2	−	+	NC	+	−	−	−	−	+	−
Vibrio	5	+	+	F	+	−	+	−	−	+	−
	48	+	+	F	+	−	+	−	−	+	−
	15	+	+	F	+	+	+	−	+	+	−
	31	+	+	F	−	+	+	−	+	+	−
	5	+	+	F	−	−	+	−	+	+	−
Pseudomonas	16	+	+	O	+	+	−	−	−	+	−
	3	+	+	O	+	+	+	−	−	+	−
	4	+	+	O	+	−	−	−	−	+	+
	4	+	+	NC	+	−	+	−	−	+	+
	3	+	+	Alk	+	−	+	+	−	+	−
	26	+	+	Alk	−	+	+	+	−	+	−
	5	+	+	Alk	−	−	+	+	−	+	−
	5	+	+	Alk	+	+	+	+	−	+	+
	4	+	+	Alk	+	+	+	+	−	+	−

[a]Positive reaction.
[b]Negative reaction.
[c]Fermentative.
[d]Alkaline reaction.
[e]Oxidative.
[f]No change.

A few isolates of *Flavobacterium* and *Achromobacter*, and all the Gram-positive bacteria, grew well in a distilled water medium; all other cultures were stenohaline. Only one third of the isolates grew at 35 C, confirming the data of Liston and Colwell (1963) on the psychrophilic nature of bacteria associated with marine animals in northern waters.

Discussion — The percentages of various types of bacteria found in the bluefish intestine agreed generally with Liston's (1957) observations on North Sea skate and sole; i.e., species of *Pseudomonas* and *Vibrio* predominated with very small populations of Gram-positive types. However, we found relatively large numbers of forms which were assigned to the Enterobacteriaceae. Our taxonomic selection for this group may be in error, or in fact represent a situation unique to the bluefish. Physiologically, our isolates resemble those studied by Colwell (1962) in Puget Sound. Our data show a higher percentage of nitrate reducers and fermenters as a result of greater numbers of vibrios, enteric bacteria, and fermentative *Achromobacter* species recovered. Conversely, the qualitative observations reported here are in sharp contrast to those of Aiso et al. (1968), who found only *Vibrio* in the intestines of plaice and jackmackerel. No attempt was made to identify *Vibrio parahemolyticus* among the bluefish isolates. None of our cultures produced H_2S, a universal characteristic of hemolytic vibrios reported by Baross and Liston (1970). Klug and DeMoss (1971) found 4–5% of bacteria isolated from the lower gut of silver salmon (*Oncorhynchus kisutch*) were indole-positive, and identified all as *Vibrio* species. Of our isolates reported in Table 1, 21% were indole-positive, and of these 77% were assigned to *Vibrio*.

If it can be presumed that the microorganisms in the digestive tract of fish are dependent primarily on the type of food most recently ingested (Seki 1969), then the data reported herein are consistent with this hypothesis since the gut microflora of the bluefish were similar to the flora of some other marine fish (e.g., skate, sole, cod; Shewan 1961) which may be prey for bluefish. No observations are available on fish indigenous to Long Island Sound. While no correlations were attempted between gut and water microbial populations, Murchelano and Brown (1970) reported that the waters of western Long Is-

land Sound have shown the following bacteria: *Pseudomonas*, 40.6%; *Achromobacter*, 28.6%; *Flavobacterium–Cytophaga*, 23.5%; *Vibrio*, 4.9%; Gram-positive and unidentified isolates, 2.4%. The relatively large percentages of pseudomonads and *Achromobacter* are in agreement with those for the bluefish isolates; however, the low percentages of vibrios and greater number of flavobacteria found in the waters are not comparable.

The Shewan scheme was found useful, but the large number of isolates encountered that were not directly identifiable by this procedure merit comment. Fermentative cultures assigned here to *Achromobacter* or the Enterobacteriaceae proved particularly difficult to identify. Shewan et al. (1960) did not find marine fermentative *Achromobacter* in an examination of a large number of marine isolates. Cleverdon et al. (1962) mentioned Gram-negative, nonmotile fermentative rods, but did not place them in any particular genus; penicillin sensitivity was not employed. Marine *Achromobacter* described by Breed et al. (1957) are not characterized by glucose fermentation. Bluefish isolates designated as Enterobacteriaceae might be considered among the "gut-group" vibrios of Liston (1957), or *Beneckea* (Bauman et al. 1971). Shewan (1961) reviewed much of the literature on bacteria associated with marine fish, and indicated the wide range of microbial genera noted in these studies and their quantitative distribution. Aiso et al. (1968) discussed some of the factors responsible for these variations and suggested that the medium selected for isolation may play a significant role. Temperature of isolation may be also cited as a variable in determining bacteria recovered. Clearly, the need for more detailed studies on fish microbiology is indicated.

Acknowledgments — The authors gratefully acknowledge the cooperation and help of Dr William A. Lund, Jr., of the Marine Research Laboratory, in the collection phases of this study.

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First Records of the Striped Bass, *Morone saxatilis*, in British Columbia Waters

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FORRESTER, C. R., A. E. PEDEN, AND R. M. WILSON. 1972. First records of the striped bass, *Morone saxatilis*, in British Columbia waters. J. Fish. Res. Bd. Canada 29: 337–339.

Two specimens of the striped bass (*Morone saxatilis*) were taken in British Columbia waters in 1971. One was taken off Port San Juan (48°30′N, 124°30′W) and one in Barkley Sound (48°58′N, 125°03′W). Previous most northerly published record for the Pacific coast was from Puget Sound, Washington.

FORRESTER, C. R., A. E. PEDEN, AND R. M. WILSON. 1972. First records of the striped bass, *Morone saxatilis*, in British Columbia waters. J. Fish. Res. Bd. Canada 29: 337–339.

Deux spécimens de bar d'Amérique (*Morone saxatilis*) furent capturés dans les eaux de la Colombie britannique en 1971: le premier, au large de Port San Juan (48°30′N., 124°30′O.) et le second, dans le détroit de Barkley (48°58′N., 125°03′O.). Les signalements publiés antérieurement désignaient le détroit de Puget comme limite nord de répartition de cette espèce sur la côte du Pacifique.

Received September 27, 1971

IN early July, 1971, a specimen of the striped bass, *Morone saxatilis*[2], was caught by gillnet near Ecoole (48°58′N, 125°03′W) in Barkley Sound, B.C., by Capt J. D. Kendrew. On August 17, 1971, a second specimen was captured in a gillnet off Port San Juan, Vancouver Island (48°30′N 124°30′W), by Capt John Toyodo of the *Canada 101*. These are the first known records for British Columbia waters.

Materials and Methods — Identifications were made with the aid of a key to California fishes (Roedel 1953). Both fish were spent females, 59 and 61 cm in total length and in their fifth year of age (aged from scales). Description according to the pattern of Leim and Scott (1966) follows:

Description — Body somewhat elongate but stout, greatest depth about 4.7 in total length under middle of spinous dorsal, slightly compressed, caudal peduncle stout. Head 3.6–3.8 in total length, bluntly pointed, slightly compressed, mouth terminal, lower jaw projecting slightly, angle of mouth in front of eye, teeth small, two parallel patches on base of tongue, also present on jaws, vomer, and palatines; two backwardly-directed, weak spines on margin of each gill cover, preopercle weakly serrate along edge. Eye 8 in head. Fins; dorsals (2) first IX, stout spines connected by membrane, fourth spine longest, 2.2–2.5 in head, first and last spines very short, others intermediate, fin located over tip of pectoral, second dorsal I, 12, first rays equal or shorter than longest spine in first dorsal, decreasing posteriorly to less than half longest ray, located immediately behind spinous dorsal, its base about the same length as that of spinous dorsal and $\frac{2}{3}$ of head length; caudal heavy, slightly forked; anal III, 11, first spine short, second spine longer, third spine longest, and 3.8–4.2 in head, soft rays similar in length to second dorsal, base of fin $\frac{3}{4}$ length of base of second dorsal, terminating slightly behind second dorsal; pectoral 16–17, moderate, located below midline behind gill opening, length 2.2 in head; pelvics I, 5, triangular, ventral, base slightly behind base of pectoral, equal to pectoral in size. Lateral line present. Scales large, ctenoid.

Most prominent features of the fish were the eight horizontal dark stripes (Fig. 1). In the Barkley Sound specimen there was a very faint suggestion of a ninth stripe. The stripes above the lateral line were longer than those below, the bottom stripe ended before the anal fin and none of the stripes extended onto the head.

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[2]In the bulk of the recent scientific literature the striped bass is called *Roccus saxatilis*. However, it has recently been assigned to the family Percichthyidae (temperate basses) and, on the basis of precedence in nomenclature, called *Morone saxatilis* (Amer. Fish. Soc. 1970).

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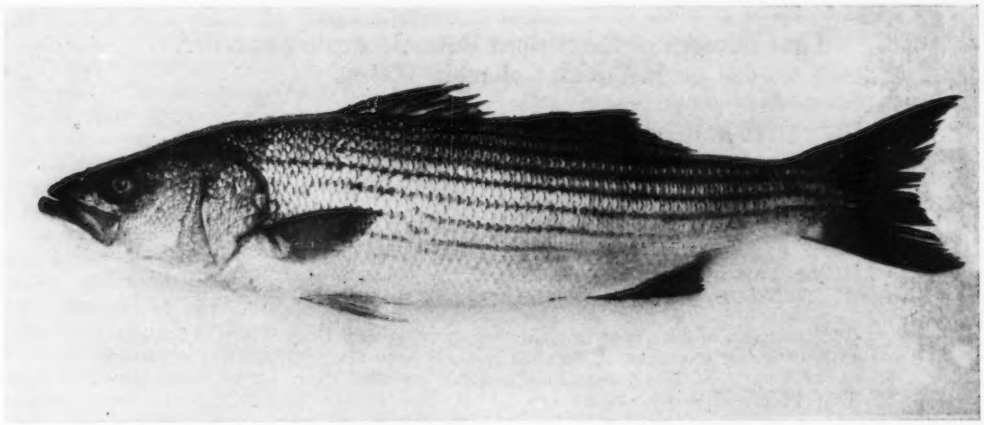

FIG. 1. Striped bass, *Morone saxatilis*, 608 mm total length, taken by gillnet August 17, 1971, off Port San Juan, British Columbia. Photo by C. J. Morley.

Discussion — The striped bass on the Pacific coast is an introduced species which has flourished remarkably since initial plantings in 1879 and 1882 in the area of the Sacramento River delta, California. These gave rise to a commercial fishery up until 1935, and since that time to an important sport fishery in the delta area. Within 20 years of initial plantings the range of the species had extended to Southern Oregon and a few years later to the mouth of the Columbia River (Smith 1910). Around 1922 a small commercial fishery developed at Coos Bay, Oregon (Morgan and Gerlach 1950) which has continued to the present time. Small numbers were taken at the mouth of the Columbia River at least up until 1948 (Oreg. Fish. Comm. 1948) but thereafter were uncommon. The most northerly occurrence previously reported (Seattle Times, April 30, 1968) was the capture of a 37 lb specimen on April 28, 1968, in Hood Canal, Puget Sound (De Lacy personal communication).

The northern range of stocks of striped bass capable of supporting a fishery appears to be limited by environmental factors. Temperatures of 60 F (15.6 C) and above are believed necessary for spawning which occurs from April in California (Calhoun 1950) to June in Oregon (Morgan and Gerlach 1950). In addition, an extensive tidal estuary appears required for a nursery area and wintering ground (Calhoun 1952). The Fraser River and estuary in British Columbia would appear to be suitable habitat for striped bass in all respects except water temperature. Temperatures of 60 F are not reached in the Fraser until late June or July (Tully and Dodimead 1957), i.e., much later than time of spawning in California, later than spawning time in Oregon, and presumably later than similar temperature is reached in the Columbia River. It thus seems highly improbable that the striped bass will become established in British Columbia waters. Occasional stragglers from more southern waters should not be unexpected particularly when there is above average northward protrusion of warm water off the British Columbia coast such as happened in mid-August, 1971 (U.S. Department of Commerce 1971).

The Port San Juan specimen has been deposited in the museum of the Institute of Animal Resource Ecology at the University of British Columbia (Cat. No. BC 71-28), while the Barkley Sound specimen is now in the collection of the British Columbia Provincial Museum.

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A Simple Fish Tag Suitable for Long-Term Marking Experiments

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WHITE, W. J., AND R. J. BEAMISH. 1972. A simple fish tag suitable for long-term marking experiments. J. Fish. Res. Bd. Canada 29: 339–341.

A simple, inexpensive fish tag that allows for growth of the fish is described. Growth rates of smallmouth bass were not significantly affected by tagging. The rate of retention on smallmouth bass was much higher than that for a tag described by Fraser but rates of retention of the two tags on largemouth bass were not significantly different. Estimated rates of tag loss were 15% after 1 year for smallmouth bass and 17% after 3 years for largemouth bass. Observed tag losses from white suckers over 3 years were only 0.6%.

Using this method, two or three persons can conveniently tag fish at a rate of approximately 30 per hour.

WHITE, W. J., AND R. J. BEAMISH. 1972. A simple fish tag suitable for long-term marking experiments. J. Fish. Res. Bd. Canada 29: 339–341.

Les auteurs décrivent une marque simple et peu dispendieuse qui tient compte de la croissance du poisson. Le marquage n'affecte pas sensiblement le rythme de croissance des achigans à petite bouche. Le pourcentage de rétention de cette marque par les achigans à petite bouche est beaucoup plus élevé que celui de la marque décrite par Fraser, mais il n'y a pas de différence significative entre les taux de rétention des deux marques par les achigans à grande bouche. Le taux de perte de marques est estimé à 15%, après 1 an, chez les achigans à petite bouche, et à 17%, après 3 ans, chez les achigans à grande bouche. Les pertes de marques observées chez les catostomes noirs communs ne sont que de 0.6% après 3 ans.

Cette méthode permet à deux ou trois personnes de marquer facilement 30 poissons à l'heure.

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IN 1967 and 1968, studies on populations of white suckers (*Catostomus commersoni*), largemouth bass (*Micropterus salmoides*), and smallmouth bass (*Micropterus dolomieui*) entailed considerable tagging. This note describes the preparation and application of the new type of tag used and gives data on the usefulness of the tag.

The label consisted of a piece of spaghetti tubing 25 mm long with an outside diameter of 2.0 mm (Floy Tag Co.). For smaller fish the length of the label was reduced. The label was fastened to the fish by approximately 10 cm of polypropylene monofilament (0.3 mm diam, breaking strength 4.4 kg).

Application of tag — When applied to white suckers (Fig. 1A) the tag resembled Saunder's (1968) modification of the Swedish smolt tag (Carlin 1955). The monofilament was sewn with a needle under the dorsal fin rays between the pterygiophores, out through the skin on the opposite side, then back through the flesh to the original side about 1 cm from the insertion point. The two strands were tied in a surgeon's knot so that the monofilament was taut but did not pinch the skin. The label was threaded over the two strands of monofilament that were then knotted behind it. The label was then forced back so that the distal end covered the knot. The free ends of the monofilament were fused to the tubing in an alcohol flame.

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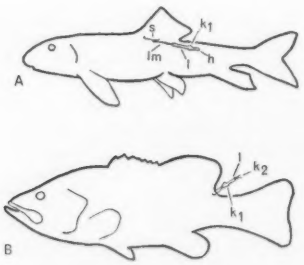

FIG. 1. Appearance and location of tag on A, white sucker and B, smallmouth bass. h, heat seal; k_1, knot of monofilament inside label; k_2, large knot of monofilament at distal end of label; 1, label; 1m, length of monofilament to allow for growth; s, surgeon's knot.

Bass were tagged by passing the monofilament only once through the muscle about 1–1.5 cm deep immediately behind the dorsal fin and then securing the two strands with an overhand knot (Fig. 1B). The tubing was threaded over the monofilament as far as the knot, and a second overhand knot was tied hard against the distal end of the tubing to retain it. Excess monofilament was cut away with scissors. A heat seal was not used when tagging bass.

The length of monofilament between the surgeon's knot and the bottom of the label allowed the fish to grow over the knot without covering any part of the label. This length should be greater for younger fish than for older ones.

Tubing that was previously soaked in a solution of malachite green reduced algal growth on the tubing and fungus growth on a fresh wound. Two persons conveniently performed all of the tagging operations. Prior to tagging, suckers were anaesthetised in M.S. 222, but bass were tagged without anaesthetic with no apparent ill effects. The tags were applied at a rate of approximately 30 per hour.

Tagging wounds of suckers healed within several months and after 1 year the loop of monofilament distal to the knot and label was partly covered with tissue. After 2 years it was frequently covered completely. Bass healed somewhat more slowly and some wounds were irritated unless the loop passing through the flesh was loose.

Usefulness of tag — Bass were fin-clipped for ready identification of recovered fish that lost their tags, and all suckers taken in the recovery program were examined for evidence of tagging wounds. Of 650 recoveries of tagged suckers in the 3 years after tagging, three fish had lost the spaghetti tubing label and one had lost the entire tag. Of 633 recaptures made before August 14 in the year of tagging smallmouth bass, five had lost their tags. In the next year, 16 of 108 bass recaptured (15%) had lost their tags. These rates of tag loss are low for this species. Fraser (1955) estimated that 80% of smallmouth bass tagged in various ways had lost their tags by the following year.

The suitability of the spaghetti tag for marking largemouth bass was compared directly with that of the tag used in 1949 by Fraser (1955) on smallmouth bass. Fraser's tag consisted of an oval celluloid disc 0.5×0.3 inches. A 9-inch length of nylon monofilament (6-lb test) was inserted through a hole in the label and tied with a clinch knot. The monofilament was passed through the flesh immediately behind the dorsal fin with a needle, brought around as tightly as possible, returned through the hole in the label, and secured to the label by two half-hitches. Excess monofilament was cut off with scissors.

From August 2 to 8, 1967, 98 larghmouth bass were marked with spaghetti tags and 103 with Fraser's tag at Nogies Creek, Ontario. The percentages of fish marked by these methods, which were recaptured at least once from 1967 through 1970, did not differ significantly ($P > 0.05$) in any of these years. The numbers recaptured at least once in the various years, and (in parentheses) the expected numbers along with the chi-square values, were:

Year	1967	1968	1969–70
Spaghetti tag	9(10.7)	23(23.8)	7(5.8)
Fraser's tag	13(11.2)	26(25.0)	5(6.1)
Chi-square	0.54	0.066	0.45

Therefore, there is no evidence of a difference in either tag losses or tagging mortality between the two groups of fish tagged by these methods.

Losses of tags of each type from largemouth bass appeared to be few. The total losses of the two tags from 1967 through 1969 were:

Years after tagging	0	1	2	Total
No. of recaptures	268	264	64	596
Tags lost (%)	0	9.0	17.2	5.9

Bass are commonly tagged by means of a strap encircling the mandible (Forney 1961). However, Youngs (1958) found that a strap tag around the mandible significantly reduced the growth rate of smallmouth bass.

The growth rate of smallmouth bass marked with the spaghetti tag was compared with that of unmarked bass using the method of comparison employed by Youngs. The regression of length at recapture on length at tagging of 38, age VII, smallmouth bass gave a curve described by the equation:

$$L_8 = 0.78L_7 + 3.69$$

where: L_8 is the length at recapture; L_7 is the length

at age VII. This curve represents the growth rate of tagged bass at age VII.

The mean length at age VIII of 123 unmarked bass was 13.8 inches. The mean length at age VII of 249 unmarked bass was 13.0 inches. These lengths, substituted for L_8 and L_7, respectively, satisfy the above equation almost exactly. Therefore, the spaghetti tag appears not to have affected the growth rate of tagged smallmouth bass.

The tag has also been used successfully on northern pike *Esox lucius* with few tag losses (J. Casselman personal communication).

Tagging did not appear to interfere with spawning of suckers. Of 296 tagged on the spawning grounds in 1967, 95 were recaptured within 3 weeks at least once and many were recaptured several times.

This tag appears suitable for long-term studies of suckers, bass, and probably a number of other fishes.

Acknowledgments — The authors appreciate the assistance of Dr F. E. J. Fry in the design and application of the tag, and for providing data on the tagging of largemouth bass at Nogies Creek, Ontario. Mr R. S. Dursley was responsible for operations at Nogies Creek. Financial support was provided by grants from the National Research Council of Canada, the Fisheries Research Board of Canada, and the Canadian National Sportsmen's Show.

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A Diver-Operated Plankton Collector

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ENNIS, G. P. 1972. A diver-operated plankton collector. J. Fish. Res. Bd. Canada 29: 341–343.

A plankton collecting apparatus was devised by strapping together two diver-towing vehicles and mounting a 50-cm plankton net ahead of them. It can be operated at the surface by a snorkel diver or under water by a scuba diver.

ENNIS, G. P. 1972. A diver-operated plankton collector. J. Fish. Res. Bd. Canada 29: 341–343.

Un échantillonneur de plancton a été fabriqué en ceinturant ensemble deux traîneaux de plongeur et en montant à l'avant un filet à plancton de 50 cm. L'appareil peut être manoeuvré par un plongeur équipé d'un tuba en surface, ou d'un scaphandre autonome en profondeur.

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THE main difficulties associated with plankton collecting in shallow coastal areas include depth control over relatively shallow water and towing close to the bottom, especially where the bottom is uneven. It was to alleviate these particular difficulties that the diver-operated plankton collector described here was devised.

Materials and methods — The apparatus is propelled by two battery-powered, motor-driven diver-towing vehicles (DPV MK-I; Farallon Industries, Belmont, California). The specifications include: size, 33 inches (83.8 cm) long, 8 inches (20.3 cm) diam; weight, 45 lb (20.4 kg) in air; motor, high efficiency permanent magnet motor in sealed compartment; power, two 12 V DC, 14 amp/hr batteries; speed and duration, 2½ knots (4.6 kph) for 1 hr continuous operation (batteries fully charged); operating depth, 300 ft (91.4 m) capability.

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The vehicles are strapped together (Fig. 1A, B) with double semicircular aluminum clamps bolted together on both sides of each vehicle. A supporting structure attached to the top part of a 50 cm plankton net by means of a specially designed clamp (Fig. 1C) is shaped to position the net about 10 inches (25.4 cm) in front with the top of the net about 8 inches (20.3 cm) above the vehicles. This structure is bolted to the

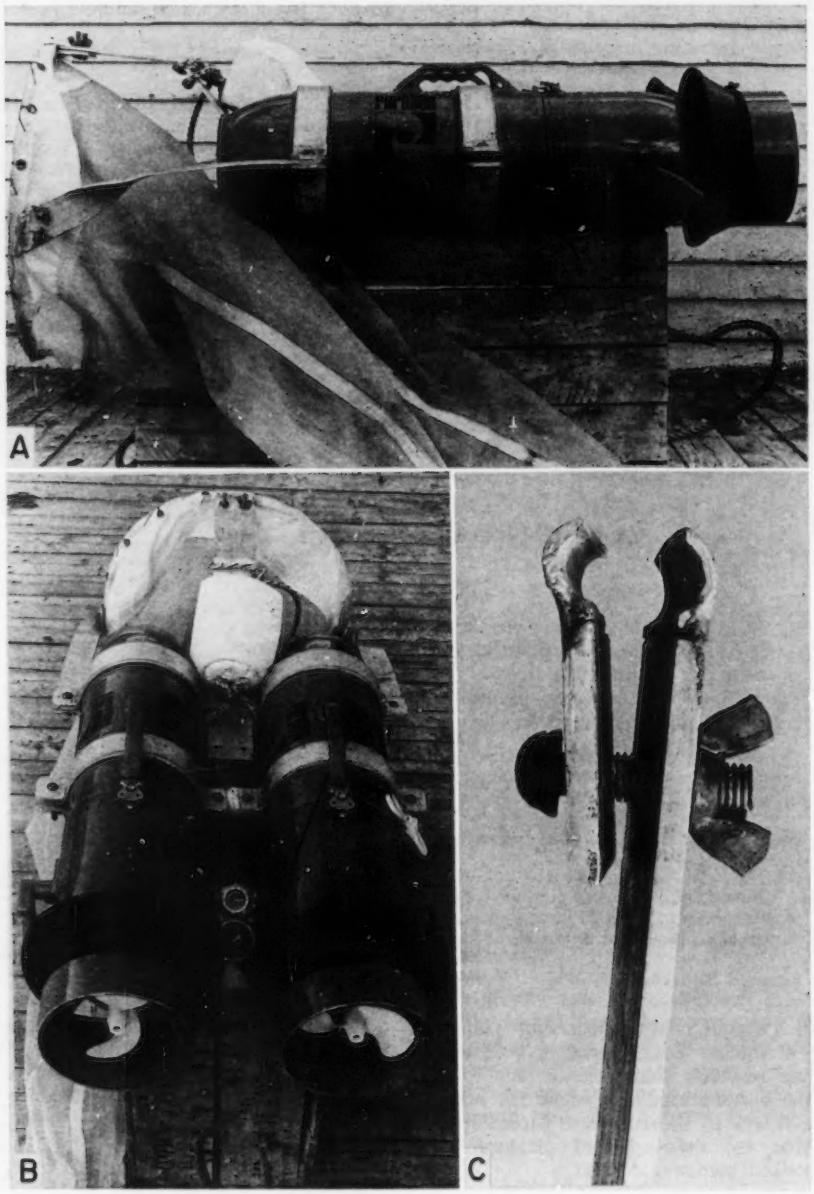

FIG. 1. Side (A) and top (B) views of apparatus. (C) Clamping mechanism for attaching ring of plankton net.

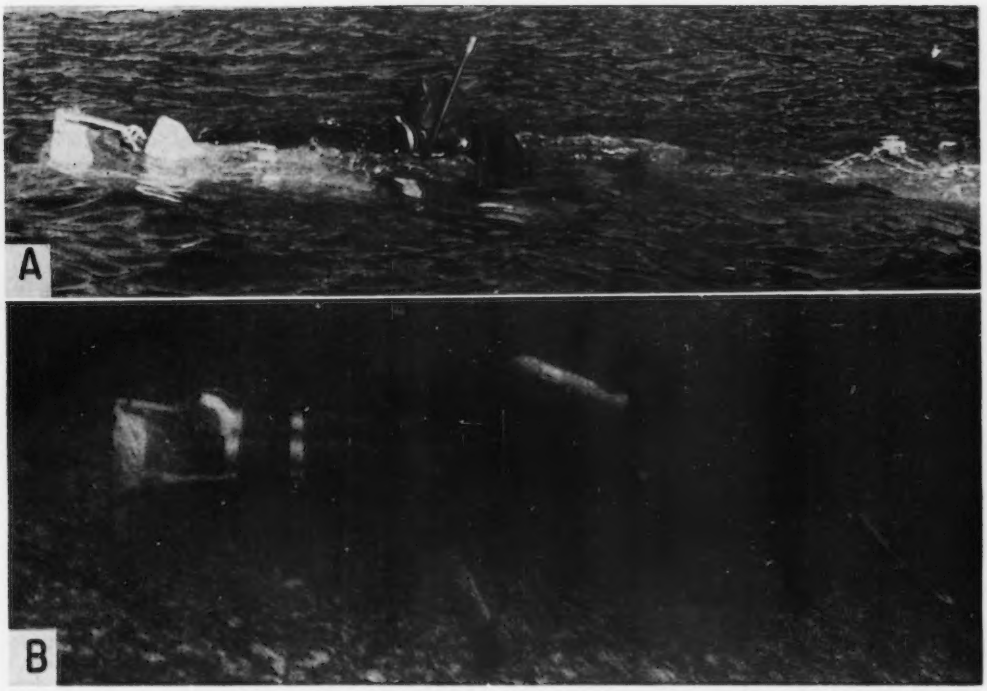

FIG. 2. Apparatus being operated (A) at the surface and (B) under water.

forward set of semicircular clamps between the two vehicles. A similar supporting structure is bolted to the forward set of clamps on the outside of each vehicle to support the net at the sides. Buoyancy material is attached near the front of the vehicles to counteract the weight of the net and supporting structures so that the apparatus floated level at the surface.

Results and discussion — In actual use the apparatus has performed well. It can be used at the surface (Fig. 2A) by a snorkel diver and underwater by a scuba diver (Fig. 2B) and can readily be maintained at a uniform depth by a diver. It has been used to depths of 90 ft (27.4 m). To prevent the net from fishing the apparatus can be pushed or pulled backwards to and from the depth at which it is to be operated. It can be operated at the surface and under water at approximately 2 mph (3.2 kph) with a number 2 mesh (366 μ) plankton net by a 190 lb (86.2 kg) diver wearing approximately 85 lb (38.6 kg) of scuba diving equipment. With full scuba equipment individual tows of 10–15 min duration and with snorkel equipment only tows of 30 min duration can be made without undue strain on the diver's wrists and forearms. We have found that the batteries maintain full power for only about 30 min. Extra batteries would increase the number of tows that could be made during a dive. When the apparatus is brought to the surface at the end of a tow it takes about 3 min to wash down the net and attach a clean strainer in preparation for the next tow.

Despite the slow speed of the apparatus it does collect the smaller planktonic organisms (including copepods, amphipods, all stages of decapod crustacean larvae, and newly-hatched fish larvae), apparently quite efficiently. In previous years in the same area the same kinds of plankton were collected in the same size net towed behind a boat moving about twice as fast.

More powerful models of the vehicle (DPV MK-II and MK-III) are now available and would probably increase the overall efficiency of a plankton collecting project using such an apparatus.

Acknowledgments — I wish to thank G. Dawe for assistance in designing the apparatus and in carrying out the initial tests.

The Deepwater Sculpin, *Myoxocephalus quadricornis thompsoni*, New to Alberta, Canada

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National Museum of Natural Sciences
National Museums of Canada, Ottawa, Ont.

J. C. Ward

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National and Historic Parks Branch, Calgary, Alta.

McAllister, D. E., and J. C. Ward. 1972. The deepwater sculpin, *Myoxocephalus quadricornis thompsoni*, new to Alberta, Canada. J. Fish. Res. Bd. Canada 29: 344–345.

Specimens of the deepwater sculpin from Upper Waterton Lake provide the first record for Alberta and extend the known range over 450 miles to the southwest.

McAllister, D. E., and J. C. Ward. 1972. The deepwater sculpin, *Myoxocephalus quadricornis thompsoni*, new to Alberta, Canada. J. Fish. Res. Bd. Canada 29: 344–345.

Le chabot de profondeur est signalé pour la première fois pour la province d'Alberta de deux specimens du Lac Upper Waterton qui étend l'aire de répartition plus de 450 milles aux sud-ouest.

Received August 11, 1971

The deepwater sculpin, *Myoxocephalus quadricornis thompsoni* (Girard), is known in a diagonal band of lakes scattered across northern North America from the Great Lakes to Great Bear Lake, or north to lakes on Victoria Island, N.W.T., if populations from the latter are included in this subspecies (McAllister 1961; McPhail and Lindsey 1970). In part, the scattered nature of its known distribution is due to the infrequent sampling with suitable gear in its usually deepwater habitat and recent collecting in deep water has extended their known range (Koshinsky 1965; Martin and Chapman 1965; Delisle and Van Vliet 1968; McPhail and Lindsey 1970). But in part, it is also due to the spotty occurrence of lakes with suitable environmental conditions and the necessary historical connections with proglacial lakes. Records of the species from Alberta, southern Saskatchewan, and Montana have been lacking (Scott and Crossman 1969; Gould and Brown 1970; Paetz and Nelson 1970). This note provides the first report of the deepwater sculpin for the Saskatchewan drainage and Alberta. Nomenclature provisionally follows McPhail and Lindsey (1970).

Two specimens of *Myoxocephalus quadricornis thompsoni* were caught in Upper Waterton Lake, Waterton National Park, southwestern Alberta, by K. Goble in August 1966. Upper Waterton Lake, the more southerly, and Lower Waterton Lake, separated by a narrow neck called the Bosporus, are together called the Waterton Lakes and flow northward into the Oldman River, a tributary of the South Saskatchewan River. The depth of the collection was not recorded, but below 50 m the temperature is about 5 C the year-round (Cuerrier and Schultz 1957).

Characters of the two specimens, 27 and 48 mm in standard length, follow. The four preopercular spines with the uppermost 2.2 and 4% of the standard length (respectively, for the small and large specimens), the presence of a gap between the dorsal fins, and the gill membranes forming a fold across the isthmus, identify the specimens as the deepwater sculpin. The papillae on the top of the head behind the eyes were large and numerous and the pigment was slightly darker, thus resembling specimens on hand from Keller Lake, N.W.T., rather than those from Quebec, Ontario, and Michigan. Aside from this, no prominent differences were noted between the Waterton specimens and other populations.

The Upper Waterton Lake record is over 725 km (450 miles) to the southwest of the nearest known locality, Lac La Ronge, central Saskatchewan. It has been hypothesized that the deepwater sculpin dispersed following Wisconsin deglaciation in proglacial lakes (McAllister 1961). The Geological Survey of Canada *Glacial Map of Canada* (Number 1253A, 1968), contrary to Ricker (1959), does not show Waterton Lakes as lying in a proglacial lake bed, although one is shown some 8–16 km (5–10 miles) to the north. It is possible that during the Wisconsin glaciation a southward flowing outlet from this pro-

Printed in Canada (J2267)

glacial lake provided access to Waterton Lakes for the deepwater sculpin, and for the two glacial relict crustaceans *Mysis relicta* and *Pontoporeia affinis* reported from Waterton Lakes by Ricker (1959). The deepwater sculpin specimens are catalogued in the ichthyology collection of the National Museum of Natural Sciences, Ottawa, as NMC71-217. It it likely that the deepwater sculpin occurs in that portion of Upper Waterton Lake that lies in Montana.

CUERRIER, J. P., AND F. H. SCHULTZ. 1957. Studies of lake trout and common whitefish in Waterton Lakes, Waterton Lakes National Park, Alberta. Can. Wildlife Serv. Wildlife Manage. Bull. Ser. 3(5): 1–41.

DELISLE, C., AND W. VAN VLIET. 1968. First records of the sculpin *Myoxocephalus thompsonii* and *Cottus ricei* from the Ottawa Valley, southwestern Quebec. J. Fish. Res. Bd. Canada 25: 2733–2737.

GOULD, W. R., AND C. J. D. BROWN. 1970. Distribution of sculpins (Cottidae) in Montana. Copeia 1970: 594–595.

KOSHINSKY, G. D. 1965. Limnology and fisheries of five Precambrian headwater lakes near Lac la Ronge, Saskatchewan. Sask. Dep. Natur. Resour. Fish. Br. Rep. 7: 1–52.

MARTIN, N. V., AND L. J. CHAPMAN. 1965. Distribution of certain crustaceans and fishes in the region of Algonquin Park, Ontario. J. Fish. Res. Bd. Canada 22: 969–976.

MCALLISTER, D. E. 1961. The origin and status of the deepwater sculpin, *Myoxocephalus thompsonii*, a nearctic glacial relict. Nat. Mus. Can. Bull. 172: 44–65.

MCPHAIL, J. D., AND C. C. LINDSEY. 1970. Freshwater fishes of Northwestern Canada and Alaska. Fish. Res. Board Can. Bull. 173: 1–381.

PAETZ, M. J., AND J. S. NELSON. 1970. The fishes of Alberta. The Queen's Printer, Edmonton, Alta. 282 p.

RICKER, K. E. 1959. The origin of two glacial relict crustaceans in North America, as related to Pleistocene glaciation. Can. J. Zool. 37: 871–893.

SCOTT, W. B., AND E. J. CROSSMAN. 1969. Checklist of Canadian freshwater fishes with keys for identification. Roy. Ont. Mus. Misc. Publ. 104 p.

Recent Articles on FRB Investigations Published in Other Periodicals

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles, which henceforth may be obtained in reprint form only from the author or originating FRB establishment. The number following each title refers to the FRB establishment listed below.

(1) Fisheries Research Board of Canada
Biological Station
P.O. Drawer 100
Nanaimo, British Columbia

(2) Fisheries Research Board of Canada
Vancouver Laboratory
6640 N.W. Marine Drive
Vancouver 8, British Columbia

(3) Fisheries Research Board of Canada
Pacific Environment Institute
4160 Marine Drive
West Vancouver, British Columbia

(4) Fisheries Research Board of Canada
Freshwater Institute
501 University Crescent
Winnipeg 19, Manitoba

(5) Fisheries Research Board of Canada
Arctic Biological Station
P.O. Box 400
Ste. Anne de Bellevue, Quebec

(6) Fisheries Research Board of Canada
Biological Station
St. Andrews, New Brunswick

(7) Fisheries Research Board of Canada
Marine Ecology Laboratory
Bedford Institute
P.O. Box 1006
Dartmouth, Nova Scotia

(8) Fisheries Research Board of Canada
Halifax Laboratory
P.O. Box 429
Halifax, Nova Scotia

(9) Fisheries Research Board of Canada
Biological Station
St. John's, Newfoundland

1607. RICKER, W. E. 1969. Food from the sea, p. 87–108. *In* Resources and man, a study and recommendations. Report of the Committee on Resources and man, U.S. National Academy of Sciences, Preston Cloud, Chairman. W. H. Freeman and Co., San Francisco, Calif. (1)

1608. LITCHFIELD, C., R. G. ACKMAN, J. C. SIPOS, AND C. A. EATON. 1971. Isovaleroyl triglycerides from the blubber and melon oils of the beluga whale (*Delphinapterus leucas*). Lipids 6: 674–681. (8)

1609. COOTE, A. R., I. W. DUEDALL, AND R. S. HILTZ. 1971. Automatic analysis at sea, p. 347–351. Advances in automated analysis. Technicon International Congress. Volume II, Industrial Analysis, Thurman Associates. (7)

1610. KABATA, Z., A. RAIBAUT, AND O. K. BEN HASSINE. 1971. *Eubrachiella mugilis* n. sp., un copepode parasite de muges de Tunisie. Bull. Inst. Nat. Sci. Tech. Oceanogr. Peche 2: 87–93. (1)

1611. IDLER, D. R., L. M. SAFE, AND E. F. MACDONALD. 1971. A new C-30 sterol (Z)-24-propylidenecholest-5-en-3B-OL (29-methylisofucosterol). Steroids. 18: 545–553. (8)

1612. NYMAN, O. L., AND D. H. SHAW. 1971. Molecular weight heterogeneity of serum esterases in four species of salmonid fish. Comp. Biochem. Physiol. 40B: 563–566. (9)

1613. SHAW, D. H. 1971. Neutral carbohydrates in the milk of the Bottlenose dolphin (*Tursiops truncatus*). Carbohyd. Res. 19: 419–422. (9)

1614. ARMSTRONG, F. A. J., AND J. F. UTHE. 1971. Semi-automated determination of mercury in animal tissue. Atomic Absorption Newsletter 10: 101–103. (4)

1615. SAETHER, O. L. 1971. Notes on general morphology and terminology of the Chironomidae (Diptera). Can. Entomol. 103: 1237–1260. (4)

1616. ODENSE, P. H., T. C. LEUNG, AND Y. M. MAC DOUGALL. 1971. Polymorphism of lactate dehydrogenase (LDH) in some gadoid species. Rapp. Proces-Verbaux Reunions Cons. Perma. Int. Explor. Mer 161: 76–79. (8)

1617. SAETHER, O. A. 1971. Four new and unusual Chironomidae (Diptera). Can. Entomol. 103: 1799–1827. (4)

Additional FRB Publications

The Fisheries Research Board of Canada also publishes a series of *Bulletins*, each on a specific topic. These are for sale by Information Canada, Ottawa, and remittances must be in advance, payable in Canadian funds to the order of the Receiver General of Canada. *Bulletins* are also available from local booksellers and Information Canada bookshops throughout Canada.

The *Annual Report* of the Board and the biennial *Review* of investigations are available free, on request. All publications may be referred to at Board establishments located at: Ottawa; Nanaimo and Vancouver, B.C.; Winnipeg, Man.; Ste. Anne de Bellevue, Que.; St. Andrews, N.B.; Halifax and Dartmouth, N.S.; and St. John's, Nfld

L'Office des recherches sur les pêcheries du Canada publie également une série de *Bulletins*, chacun traitant sur un sujet spécifique. Les publications de l'ORP sont vendues par Information Canada à Ottawa. Les remises, payables d'avance en monnaie canadienne, doivent être établies à l'ordre du Receveur général du Canada. Les *Bulletins* sont aussi en vente chez votre libraire et dans les librairies d'Information Canada.

Vous pouvez obtenir le Rapport Annuel et la Revue biennale gratuitement. On peut consulter ces ouvrages aux établissements de l'Office situés à Ottawa (Ont.), à Nanaïmo et à Vancouver (C.-B.), à Winnipeg (Man.), à Ste-Anne-de-Bellevue (P.Q.), à St-Andrews (N.-B.), à Halifax et à Dartmouth (N.-E.), et à St-Jean (T.-N.).

Journal
Fisheries
Research
Board
Canada

Guide to Authors

Details on typing and other items in preparing copy are given in a guide for typists. Also, a list of recommended spellings of about 100 words common in fisheries journals is available from the Office of the Editor.

Editorial Practices

Abstracts should be provided in both English and French.

The *Style Manual for Biological Journals* (2nd ed. American Institute of Biological Sciences, 2000 P St. NW., Washington, D.C.) is, with few exceptions, used as the authority in matters of form. *Webster's Third New International Dictionary* is the standard for spelling and division of words in English; *le Grand Larousse Encyclopédique*, for those in French. Exceptions are made for manuscripts that follow the *Oxford English Dictionary* entirely. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. Manuscript reports are included in the list of references, but are identified both there and in the text by the letters "MS" before the year. The *Journal* follows the spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (Third Edition, 1970), Special Publication No. 6 of the American Fisheries Society.

Notes are distinguished from *papers* on the basis of scope or completeness, rather than quality, of the research. They may be on problems with narrow, readily defined limits; on fishing gear or methods, or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued before completion; or on preliminary findings that warrant publication before problems are resolved satisfactorily. Or they may be used to establish priority in publication. They may be organized with as much flexibility as papers except that they may have no centered headings. They should take no more than four pages in the *Journal*.

In general, *series titles* should be avoided.

Illustrations

Line drawings are preferably made with black india ink on white drawing or tracing paper or on coordinate paper with blue grids. All lines, symbols, letters, and numerals must be neat, and legible when the illustration is reduced to the appropriate size. Drawings should be grouped, when feasible, for economy of space. Originals must be submitted and should be less than 20 inches in the greater dimension for full-page illustrations, and proportionately smaller for those taking less than a page. Drawings must not be rolled for mailing.

Prints of photographs should be made on glossy paper with a wide range in tone. They should be cropped, squared, and mounted with rubber cement on white cardboard, with no space between those arranged in groups.

Proofs and Reprints

Galley proof is sent to the author, and he is responsible for detecting errors in printing as well as in content.

Fifty reprints, without covers, are supplied free. Additional copies needed must be ordered, on the form provided, when the galley proof is returned.

Checklist on Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors. The same questions are recommended to referees who review manuscripts for the *Journal*.

General

Is there new knowledge in the report worth publishing?
Are the findings, interpretations, and conclusions sound, and relevant to the purpose of the study?
If the manuscript is merely confirmatory, is it worth publishing?

Does the manuscript need to be rewritten before the work can be assessed?

Is the contribution placed in the proper perspective concerning the state of knowledge of the subject?

Is the manuscript too long?
Are all the tables and figures needed, and organized for economy of space?
Would any of the text be clearer if condensed?
Should some of the data be made available separately, in a manuscript report or at a data repository?
Should the manuscript be condensed as a Note?

Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Are summary statements given at the beginnings of sections and paragraphs, and are details in sections and paragraphs relevant to their topics?

Are there inconsistencies between tables or figures and the text, or within the text?

If the manuscript is from a thesis, does it retain characteristics common in these but not desirable in journals?

Parts of the Manuscript

Does the *title* encompass the content of the report?

Does the *abstract* give the essentials of the new knowledge?

Has the *introduction* all the important guideposts for orienting the reader?

Is review of the literature limited to defining the problem?

Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data obtained?

Are generalizations on the *results* adequate?

Are findings distinguished from inferences from them?

Is *discussion* limited to interpretation and significance of the findings?

If there are loopholes in interpretation, are they acknowledged? Should they be overcome?

Should other interpretations be recognized?

Journal of the Fisheries Research Board of Canada

Guide des auteurs

Des détails sur le tapage et certains autres item sont donnés dans le "Guide pour les secrétaires d'auteurs." Aussi, une liste d'épellations recommandées d'environ 100 mots relatifs aux articles sur les pêcheries est disponible au bureau du Directeur de la publication.

Disposition générale

Les résumés doivent être fournis en anglais et en français.

Le *Style Manual for Biological Journals* (deuxième édition, publié par l'American Institute of Biological Sciences, 2000, rue *P* N.-O., Washington, D.C.), a été adopté comme guide des auteurs. Le *Third New International Dictionary* de Webster, dans le cas de l'anglais, et le *Grand Larousse Encyclopédique*, dans le cas du français, font respectivement autorité pour l'orthographe et la séparation des mots. Une exception est faite à l'égard des travaux en anglais qui se conforment entièrement à l'*Oxford English Dictionary*. Les titres de périodiques sont abrégés selon la *Biological Abstracts*. Toute référence à la littérature doit suivre le système nom-année. Les rapports manuscrits sont inclus dans la liste des références, les lettres "MS" avant l'année les identifient dans les références et dans le texte. Le *Journal* se sert des épellations recommandées dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No 6 de l'American Fisheries Society.

Les *notes* se distinguent des écrits d'après l'étendue de la recherche plutôt que par la qualité de la recherche. Les notes peuvent être sur des travaux de recherche de portée restreinte, susceptibles de découler d'investigations plus considérables, pour la description de techniques de recherche et de méthodes de pêche, pour l'établissement de priorités de publication, et pour faire connaître les renseignements utiles tirés d'entreprises qui ont été interrompues avant d'avoir été achevées. Si la portée de la Note le permet, elle peut être disposée comme un mémoire. D'autre part, la disposition est flexible. La longueur ne doit pas dépasser quatre pages imprimées.

En général, les mémoires en série doivent être évités.

Les illustrations

Les dessins au trait doivent être exécutés à l'encre de chine sur papier à dessin blanc ou sur papier à calquer, ou sur papier à coordonnées avec quadrillage bleu. Les lignes, les symboles, les lettres et les chiffres doivent tous être propres. Ils doivent être lisibles quand ils sont réduits à la grandeur voulue pour la reproduction désirée. Les dessins doivent être groupés, si la chose est possible, de façon à utiliser tout l'espace disponible. Les originaux doivent être soumis et devraient mesurer moins de 20 pouces dans le sens le plus long pour les illustrations de pages entières, et proportionnellement plus petit pour les illustrations de moins d'une page. Les dessins doivent être postés à plat.

Les épreuves des photographies doivent être tirées sur papier glacé et accuser une gamme étendue de teintes. Elles doivent être coupées, dressées et montées, au moyen de dissolution, sur carton blanc, sans laisser d'espace entre celles qui sont disposées par groupes.

Epreuves et tires a part

Les épreuves en placards sont adressées à l'auteur et la responsabilité de toute erreur qui peut y rester lui incombe.

Cinquante tirés à part, sans couverture, sont fournis gratuitement. L'auteur peut profiter du renvoi des épreuves en placards pour commander d'autres tirés à part.

Liste de contrôles pour manuscrits

Une attention particulière portée sur les questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les rédacteurs. Les mêmes questions sont recommandées aux arbitres qui font la critique des livres pour le *Journal*.

Generalites

Est-ce que les connaissances nouvelles du rapport méritent d'être publiées?

Les découvertes, les interprétations et les conclusions sont-elles solides et pertinentes au but de l'étude?

Si le manuscrit est tout simplement corroboratif, mérite-t-il d'être publié?

Le manuscrit doit-il être récrit avant d'évaluer le travail?

La contribution est-elle placée dans une perspective appropriée relative à l'état des connaissances du sujet?

Le manuscrit est-il trop long?

Les tables et figures sont-elles toutes nécessaires et arrangées pour économiser le plus d'espace?

Le texte serait-il plus clair s'il était condensé?

Est-ce qu'une partie des données devrait être disponible séparément, soit dans un rapport ou dans un dépôt des données?

Le manuscrit devrait-il être condensé en une note?

Est-ce que la préparation du manuscrit suit la logique mentionnée dans l'introduction?

Y a-t-il des exposés sommaires au début de chaque section et paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents aux sujets?

Y a-t-il des contradictions entre les tableaux et les figures du texte, ou dans le texte même?

Si le manuscrit est tiré d'une thèse, contient-il des caractéristiques communes à cette dernière, mais indésirables dans un journal?

PARTIES DU MANUSCRIT

Le titre renferme-t-il le contenu du rapport?

Le résumé donne-t-il l'essentiel des connaissances nouvelles?

L'introduction a-t-elle tous les points importants afin d'orienter le lecteur?

Le renvoi bibliographique se limite-t-il à la définition du problème?

Les détails du matériel et des méthodes employées sont-ils limités à un minimum pour que les scientifiques comprennent le but de l'étude et puissent porter un jugement adéquat sur les données obtenues.

Les généralisations sur les résultats sont-elles adéquates?

Les conclusions sont-elles déduites des résultats?

La discussion est-elle limitée à l'interprétation et la signification de ces découvertes?

S'il y a des échappatoires dans l'interprétation, sont-elles reconnues? Devraient-elles être maîtrisées?

Devrait-on accepter d'autres interprétations?

Journal of the Fisheries Research Board of Canada

Guide for Typists Preparing Copy

Read the "Guide to Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 8.5 × 11 inches (21.5 × 28 cm). If possible, use paper with the lines numbered in the margin. Leave all margins at least 1 inch (2.5 cm) wide. Use a nylon or carbon ribbon and keep the typewriter keys clean.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize only the first word and proper names and adjectives. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numbers. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (Appendix A). Type the abstract on a separate page (Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send two copies (the ribbon copy and a carbon copy or a photocopy) to the Office of the Editor.

Tables

Examine the current volume of the *Journal* to see how tables are set up (Appendix C).

Note especially the following concerning *numbered tables*:

Type each table on a separate page, using paper without the lines numbered.

Number the tables with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, they are typed with the text, they seldom need horizontal lines, and the data are arranged in as few rows as possible (Appendix C).

Illustrations

Send the original and two clear copies of each illustration with the manuscript. At the lower left of each figure and copy, give the author's name and the figure number. Also type each caption with its figure for identification. For photographs, type this information on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas

Leave three spaces above and below lines that have much material in superscripts or subscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter l and the numeral one, and between the capital letter O and the numeral zero. Make other explanatory notes similarly.

References

Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style that is used in the *Journal* (Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list, but if an abbreviation is in doubt, type the name in full.

Spellings

A list of about 100 words common in fisheries journals is given in Appendix F.

Appendices

Appendices A to F are available on request from the Office of the Editor.

Journal
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Guide pour les secrétaires d'auteurs

Lisez le "Guide des auteurs" dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de taper ou d'arranger les détails, suivez la pratique du *Journal*.

Tapez le manuscrit sur un papier blanc et non un papier pelure, mesurant de préférence 8½ × 11 po. (21.5 × 28 cm) et laissant une marge d'au moins 1 po. (2.5 cm). Si possible, employez un papier avec des lignes numérotées dans la marge. Employez un ruban nylon ou carbone et gardez les clés du dactylo nettes.

Chaque partie du manuscrit doit être tapée à double-interligne au moins. La chose est particulièrement importante dans le cas des tableaux, légendes d'illustrations, renvois au bas de la page et listes de références bibliographiques. Evitez de souligner à moins que la matière ne soit en italique. Mettez en retrait la première ligne de chaque paragraphe du texte, ainsi que de chaque légende et renvoi.

Dans les titres et en-têtes, n'employez la majuscule que pour le premier mot, les noms propres et les adjectifs. Pour les petites majuscules, utilisez les petites lettres.

Indiquez tous les renvois au texte par des chiffres arabes en-tête. Numérotez-les consécutivement à travers le texte en commençant par ceux de la page-titre. Placez chaque renvoi immédiatement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit donner que le titre du sujet, le nom et l'affiliation de l'auteur ou des auteurs, et tout autre renvoi utile (Appendice A). Tapez le résumé sur une page séparée (Appendice B). Numérotez chaque page, débutant avec la page-titre.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et un double du travail au Directeur de la publication.

Tableaux

Consultez une copie du *Journal* pour savoir composer les tableaux et placer les lignes qui y entrent (Appendice C).

Portez une attention particulière à ce qui suit concernant les *tableaux numérotés*.

Tapez les tableaux sur des pages séparées, en utilisant du papier sans lignes numérotées.

Numérotez les tableaux avec des chiffres arabes.

Employez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, et très rarement ailleurs. N'employez jamais de lignes verticales; de préférence, laissez de l'espace supplémentaire.

Indiquez les renvois dans les tableaux au moyen de petites lettres italiques en position supérieure et tapez-les au bas de la page.

Placez les tableaux après la liste de références.

A l'endroit où un tableau est mentionné pour la première fois, tapez dans la marge "Tableau (- - -) près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, ils sont tapés avec le texte. Ils ont rarement besoin de lignes horizontales, et l'information est préparée de façons à prendre le moins de rangées possibles.

Illustrations

Joignez au manuscrit expédié le dessin original des illustrations et des photocopies en deux exemplaires.

Au bas et à gauche de chaque figure et photocopie, inscrivez le nom de l'auteur et le numéro de la figure. Aussi, tapez chaque légende avec sa figure pour fin d'identification. Pour les photographies, tapez l'information sur une lisière de papier et collez-la au dos de la photographie. N'écrivez pas et ne tapez pas sur la photographie même. Tapez ensemble sur une feuille séparée et par ordre consécutif les légendes des illustrations, et intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, tapez dans la marge "Fig. (- - -) près d'ici."

Equations, formules et expressions mathematiques

Laissez trois espaces au-dessus et au-dessous des lignes qui contiennent du matériel en positions supérieures ou en positions inférieures, et au-dessus et au-dessous d'équations et de formules. Dans les différentes expressions, placez chaque composante dans sa position appropriée (Appendice D).

Indiquez les symboles clairement. Dans la marge, épelez les lettres grecques la première fois qu'elles apparaissent et faites une distinction entre la lettre "l" et le chiffre "un" et entre la majuscule "O" et le

chiffre "zéro." Procédez de la même façon pour d'autres notes explicatives.

References

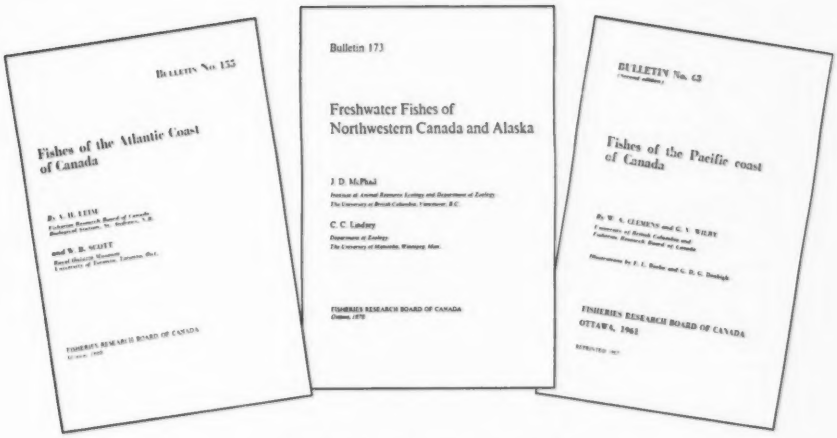
Vérifiez le texte afin d'assurer que sont mentionnées toutes les références ou renvois de la liste. Tapez, à doubles interlignes et de la façon prévue (Appendice E) pour le *Journal*, la liste de références. Les noms de journaux sont abrégés suivant la *Biological Abstracts*, mais s'il y a doute, écrivez le nom au long.

Vocabulaire

Une liste d'environ cent mots relatifs aux articles sur les pêcheries est disponible au bureau du Directeur de la publication (Appendice F).

Appendices

Les appendices de A à F sont disponibles sur demande au bureau du Directeur de la publication.



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Journal of the Fisheries Research Board of Canada

Volume 29, No. 3, March 1972

JFRBCA29(3)217–348(1972)

Some athecate hydroids from the shelf waters of northern Canada — **D. R. Calder** — 217–228

Effects of volcanic ashfalls on chemical and sediment characteristics of two Alaskan lakes — **R. J. Barsdate and R. C. Dugdale** — 229–236

Genetic and environmental sources of variation in length and weight of rainbow trout (*Salmo gairdneri*) — **D. Aulstad, T. Gjedrem, and H. Skjervold** — 237–241

Morphometrics of three sympatric arctic codfishes of the genera *Arctogadus* and *Gadus* — **J. Boulva** — 243–249

Effects of acclimation and acute temperature experience on the swimming speed of juvenile coho salmon — **J. S. Griffiths and D. F. Alderdice** — 251–264

Comparative behavior and habitat utilization of brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in northern Idaho — **J. S. Griffith Jr.** — 265–273

Parasites of fish from Lake of the Woods, Ontario — **A. O. Dechtiar** — 275–283

The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*) — **C. P. O'Connell** — 285–293

Identification of major British Columbia and Alaska runs of even-year and odd-year pink salmon from scale characters — **H. T. Bilton** — 295–301

Prolactin and growth hormone concentrations in the serum and pituitary gland of adult migratory sockeye salmon (*Oncorhynchus nerka*) — **B. A. McKeown and A. P. van Overbeeke** — 303–309

Reversible changes in adrenal cortical cell morphology and plasma hydroxycorticosteroids during freshwater portion of the spawning journey of Atlantic salmon (*Salmo salar*) — **H. L. Heyl and S. J. Carpenter** — 311–314

Effects of four insecticides on the ability of Atlantic salmon parr (*Salmo salar*) to learn and retain a simple conditioned response — **C. T. Hatfield and P. H. Johansen** — 315–321

Notes

Use of continuous recording salinity–temperature–pressure instrumentation at Ocean Station P (50N, 145W) — **C. A. Collins and D. A. Healey** — 323–327

Pathological effects in formalin-treated rainbow trout (*Salmo gairdneri*) — **C. E. Smith and R. G. Piper** — 328–329

Ecological notes on a lake-dwelling population of longnose dace (*Rhinichthys cataractae*) — **J. H. Gee and K. Machniak** — 330–332

Aerobic microflora of the bluefish (*Pomatomus saltatrix*) intestine — **J. T. Newman Jr., B. J. Cosenza, and J. D. Buck** — 333–336

First records of the striped bass, *Morone saxatilis*, in British Columbia waters — **C. R. Forrester, A. E. Peden, and R. M. Wilson** — 337–339

A simple fish tag suitable for long-term marking experiments — **W. J. White and R. J. Beamish** — 339–341

A diver-operated plankton collector — **G. P. Ennis** — 341–343

The deepwater sculpin, *Myoxocephalus quadricornis thompsoni*, new to Alberta, Canada — **D. E. McAllister and J. C. Ward** — 344–345

Recent articles on FRB investigations published in other periodicals — 347

Additional FRB publications — 348

Guides to Authors and Typists — *i–vii*

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